The

American Midland Naturalist

Founded by J. A. Nieuwland, C.S.C.

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The AMERICAN MIDLAND NATURALIST is a general biological periodical published quarterly by the University of Notre Dame. It welcomes to its pages articles of a descriptive, analytical, and experimental nature. Review articles on topics of current interest in the various fields of Biology are also welcome.

Subscription rate per year $10.00 in the U. S., Mexico, and South American countries; $11.00 elsewhere.

Address All Correspondence to:

AMERICAN MIDLAND NATURALIST
University of Notre Dame
Notre Dame, Indiana

© 1961, University of Notre Dame Press.

Entered as second-class matter at Notre Dame, Indiana. Accepted for mailing at special rate of postage provided for in Section 1103; Act of October 3, 1917, authorized on July 3, 1918.

The American Midland Naturalist

Published Quarterly by The University of Notre Dame, Notre Dame, Indiana

Vol. 65 JANUARY, 1961 No. 1

Additional Remarks on the Evolution of Trunk Musculature in Snakes

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ABSTRACT: Certain of the more important aspects of the epaxial trunk musculature of *Xenopeltis, Eryx, Calabaria, Cylindrophis* and *Tropidophis* are described. Some of these genera show a considerable departure from the basic myological pattern described for the Boidae. More important, several of these departures embody certain myological modifications paralleling the condition found in the family Colubridae.

Two major tendencies are indicated in the evolution of more complex from simpler, presumably more primitive, myological types. These are: (1) the tendency for median myological elements to become associated with more lateral ones, and (2) a tendency for anterior elements to become morphologically associated with more posterior ones, thereby lengthening considerably certain functional units through fusion of shorter muscles. A number of boid or boid-like groups have independently evolved colubrid-like myological modifications several times in the past. This phenomenon in its variety of forms is termed "myological colubridization." Details concerning the major trends in the evolution of trunk musculature are discussed, as well as their phylogenetic implications.

As a contribution to a much needed wider survey of snake myology, certain of the more important aspects of the epaxial trunk musculature of *Xenopeltis, Eryx, Calabaria, Cylindrophis* and *Tropidophis* are described. Some of these genera show a considerable departure from the basic myological pattern previously described for the Boidae. More important several of these departures embody certain myological modifications paralleling the condition found in the family Colubridae.

Introduction

Little has been published on the myology of the trunk region of snakes. Mosauer's work in 1935 remains the classic. His tripartite classification of muscle arrangement (boid, colubrid, and viperid) appears to be basically sound, though over-simplified to be useful in detailed evolutionary studies. Myological intermediacy between the typical colubrid and boid types has already been illustrated in one snake genus (Auffenberg, 1958).

I wish to thank Dr. Ernest E. Williams, Museum of Comparative Zoology, who made available most of the specimens on which this study is based.

The descriptions are based on a single adult speci-

men of each of the five genera of boid snakes examined with the exception of *Eryx johni*, where, because of their small size several specimens were examined. The myological description is meant to supplement that given by Mosauer, and follows, for the most part, his outline of presentation to facilitate comparison. Not all of the myological elements of the trunk region are discussed, but only those previously shown to be important from a comparative standpoint.

CYLINDROPHIS MACULATUS

M. Semispinalis and Spinalis (SSP, SP)

Unlike the typical boid pattern of a fused semispinalis and spinalis arising from a tendinous arch stretched between the neural spine and postzygapophysis of a single vertebra, in this genus the complex is separated, at least posteriorly, with each head arising more or less from a weakly defined tendinous arch. The spinalis arises by a raphe from the dorso-posterior surface of the M. multifidus. The semispinalis arises slightly anterior to this, partly from the dorsal surface of the arch of the same segment, and partly from another tendinous structure to be described below. A few fibers may join the two muscles along their median extent, so that they are not completely separated. Anteriorly, each muscle is provided with a thin flat tendon, directed anteriorly, medially and dorsally.

The latero-posteriorly directed arm of the tendinous arch is inserted on the latero-dorsal surface of the postzygapophysial process of the same vertebra. A much more weakly developed arm is apparently given off of the stronger arch, to run cranio-laterally, inserting on the postzygapophysial process of the preceding vertebra. Thus, the arch is attached in three areas — a neural spine, a more strongly developed arch attached to one postzygapophysis, and a more weakly developed arch extending to a more anterior postzygapophysis.

The origin of the semispinalis is by a raphe on a tendon originating on the dorso-lateral surface of a succeeding neural arch. This tendon then extends cranially to insert on the upper surface of the postzygapophysis of the vertebrae preceding the one forming the origin and insertion of the tendinous arch; thus, the tendon spans three vertebrae. Near the origin of this tendon a thin small muscle arises ventrally and slightly laterally to insert on the medio-posterior surface of the preceding vertebra. The homology of this muscle is unknown, though it appears as though it might be a separated portion of the interarticularis superior that has migrated dorsally and laterally for a short distance. Part of the origin of the semispinalis is along this tendon, where fibers run cranio-dorsally to join the main group arising on the ventral portion of the main tendinous arch. Along its length the semispinalis is also joined by fibers originating along a portion of the multifidus.

The spinalis and semispinalis both span three vertebrae, inserting by means of a long thin tendon into the caudo-dorsal edge of the neural spine of a preceding vertebra.

M. Longissimus Dorsi (ML)

This muscle is similar to that in *Constrictor* and *Sanzina*, with the origin at the cranio-lateral portion of a prezygapophysis. At about the level of the fourth vertebra cranial to its origin the muscle is replaced by a flat tendon, which divides into two parts. The medial portion inserts on the postero-dorsal portion of the neural arch of the ninth vertebra anterior to the origin of the muscle. The lower division of the tendon extends cranially and ventrally to form the medial belly of the retractor costae, inserting on the rib of the ninth vertebra.

The main difference between this series of muscles and tendons in *Sanzina*, *Constrictor* and *Cylindrophis* lie in the lengths of the myological segments. In the latter the longissimus is much shorter than in *Sanzina*, its tendon inserting on the ninth, rather than on the fourteenth rib. In *Constrictor* it inserts on the fifth rib.

M. Multifidus (MM)

In *Cylindrophis* this muscle arises from the dorsal surface of the tendinous arch and is connected to the spinalis by a raphe. It spans two vertebrae to insert on the posterior edge of the neural arch of the third vertebra. A number of fibers originating on the dorso-latero-posterior surface of the neural arch of the vertebra spanned (number 2) join the main group to continue to the common insertion on the third. Some fibers originating in the main belly of the multifidus join with those of the semispinalis.

M. Interarticularis Superior (IAS)

This muscle arises on the dorsal surface of the postzygapophysis of one vertebra, and inserts on the posterior edge of the postzygapophysis of the preceding vertebra. The arrangement is thus similar to that in *Sanzina*, but lacks the small tendinous slip which connects to the next vertebra anteriorly. The thin tendon described above under the spinalis complex, with the small muscle slip, may represent a portion of the interarticularis superior that has migrated dorsally to become associated with the semispinalis and tendinous arch.

M. Costovertebrocostalis (CV)

Unlike the condition in *Constrictor* and *Sanzina*, this muscle seems to arise in only one head; from the ventro-lateral surface of the centrum, extending caudally and laterally to insert on the costal tubercle and neck of the succeeding rib.

The remaining trunk muscles of *Cylindrophis* seem identical to those in *Constrictor*.

TROPIDOPHIS MACULATUS

M. Spinalis and Semispinalis (SP, SSP)

The spinalis of *Tropidophis* arises from the medial portion of a fairly well developed tendinous arch, running cranio-medially to the

posterior portion of a neural spine. The muscle spans nine vertebrae, and is much better developed than the semispinalis, which apparently arises by means of a tendon (shared with the interarticularis superior), and extends cranio-medially to insert on the posterior edge of a neural spine. This insertion is shared with the spinalis portion, and the two muscles become rather well interlaced over their anterior thirds. Thus, only the spinalis arises on the tendinous arch; the semispinalis having abandoned this structure by migrating laterally and then anteriorly along the interarticularis superior. The association of the interarticularis superior with the semispinalis is much more complex in *Tropidophis* than in *Sanzina*.

M. Multifidus (MM)

The multifidus spans four vertebrae, arising along almost the entire length of the tendinous arch. The muscle inserts on the caudal border of the neural arch of a more anterior element. A few fibers are interlaced with those of the interarticularis superior.

M. Longissimus Dorsi (ML)

The longissimus of *Tropidophis* is similar to that found in *Sanzina*, originating on a prezygapophysial process and extending medio-anteriorly to insert on the thirteenth vertebra from the point of origin. At the level of the tenth vertebral element, the muscle is replaced by a flat tendon which divides cranially. The medial, or dorsal portion, inserts on a neural spine, while the ventral portion runs antero-ventrally to form the partial origin of the retractor costae. Near this point a small tendon runs to the thirteenth rib anterior to that at which the longissimus originated.

M. Interarticularis Superior (IAS)

In *Tropidophis* this muscle is bifed posteriorly, but fused anteriorly, with a common insertion on a postzygapophysial process. The more medial belly of the muscle spans three vertebrae. For almost the length of one vertebra this unit is represented by a very small tendon. Near the beginning of the muscle fibers themselves (which continue anteriorly) a raphe forms the origin of the weakly developed semispinalis. The latter muscle continues dorso-cranially to form a common insertion with the spinalis. Slightly more anteriorly along the same belly of the interarticularis superior a few fibers become interlaced with those of the multifidus. At the next vertebra anterior to the origin of this belly, the lateral, and thicker belly of the interarticularis superior originates on a prezygapophysial process. Fibers from this muscle fuse with those of the medial belly to form a common insertion on the next vertebra anteriorly. Thus, the interarticularis superior of *Tropidophis* can be considered as a simple digastricus, a unit assumed to be characteristic of the Colubridae by Mosauer, though its homology with the interarticularis superior has already been indicated in *Sanzina* (Auffenberg, 1958).

ERYX JOHNI

M. Semispinalis and Spinalis (SSP, SP)

As is *Cylindrophis maculatus*, this complex is not fused, at least posteriorly, in *Eryx johni*. Furthermore, only the semispinalis originates on a tendinous arch. In this respect it differs from all other boid-like forms examined so far. From the lateral portion of the tendinous arch the semispinalis extends cranially and medially to fuse with the spinalis after passing over one vertebral segment. The spinalis arises by means of a short heavy tendon attached to the antero-lateral portion of a neural spine. It then continues anteriorly to fuse with the semispinalis. Both semispinalis and spinalis insert on the postero-lateral portion of a neural spine. From point of origin to insertion is about seven to nine vertebral segments, with most of the myological elements in the middle of the body spanning nine. The tendinous arch is complete, as in *Constrictor, Sanzina,* etc., and also serves as the origin for the multifidus. Certain strands of the interarticularis superior, particularly near the origin of this muscle, are intimately interlaced with those of the semispinalis. In this regard *Eryx* is similar to *Sanzina*, where a similar association is known to occur.

M. Longissimus Dorsi (ML)

This muscle is apparently identical to that found in *Sanzina*, with the segments of the middle of the body spanning nine vertebrae.

M. Multifidus (MM)

The multifidus arises from below the origin of the semispinalis on the same tendinous arch. From the arch the flat, well developed muscle runs cranially to insert on the posterior border of a neural arch at a distance of four vertebrae anterior to the vertebra of origin. A number of fibers originating on the dorso-latero-posterior surface of the neural arch of the vertebrae spanned (numbers two to four) join the main group to continue to the common insertion on the fifth segment. These fibers may actually arise from the belly of the intervertebralis.

M. Interarticularis Superior (IAS)

This muscle arises on the postzygapophysis of one vertebra and inserts on the posterior edge of the postzygapophysis of the preceding vertebra, as it does in most boids, and boid-like forms. However, as indicated above, fibers near the point of origin are connected with those of the spinalis complex, as in *Sanzina*. In addition the interarticularis superior seems to possess a second belly lateral to the one involved with the semispinalis. However, the specimens available for study were quite small, and the exact nature of this association needs clarification.

CALABARIA REINHARDTI

M. Semispinalis and Spinalis (SSP, SP)

This complex is fused in *Calabaria,* arising from a strong tendinous arch on one vertebra and inserting into the posterio-lateral portion of the neural spine of a vertebra nine segments cranially. As in *Sanzina* and *Eryx,* the interarticularis superior sends some fibers into the lateral portion of the semispinalis. Mosauer, who apparently examined a specimen of *Calabaria,* did not mention this association. However, unless specifically searched for this connection is difficult to see.

M. Longissimus Dorsi (ML)

This muscle in *Calabaria* is seemingly identical to that in *Sanzina,* and covers nine segments.

M. Multifidus (MM)

The origin of this muscle does not seem to be on a tendinous arch, but on the cranio-lateral portion of the neural spine of one vertebra, extending cranially and laterally to span another vertebra, to insert in a normal fashion on the third. This is the only boid or boid-like form examined in which the multifidus originates in this fashion. The muscle has evidently migrated medially off of the tendinous arch, and onto the neural spine.

M. Interarticularis Superior (IAS)

The origin and insertion of the interarticularis in this genus seems to be normal. A number of fibers form a simple association with the semispinalis. The muscle is only one segment in length.

XENOPELTIS UNICOLOR

M. Semispinalis and Spinalis (SSP, SP)

In *Xenopeltis* this complex is unlike any that I have seen in any other snake. The semispinalis and spinalis portions are essentially fused. Each fused, major unit arises from a fairly well developed tendinous arch stretched between the lateral portion of the neural arch and the neural spine, in a rather normal manner for boid, or boid-like forms. However, additional muscle slips are contributed to the main belly from tendinous arches on preceding and succeeding vertebrae. At least two vertebrae anteriorly contribute such additional fibers, and one posteriorly. The main body of the fused complex covers thirteen to fourteen vertebrae. Each tendinous arch also serves as a point of origin for the multifidus. From the neural spine a very weakly developed tendinous arch stretches to the postero-dorsal portion of the postzygapophysial process of the preceding vertebra. This arrangement is very similar to the one described

above for *Cylindrophis*. This weaker arch is below the main body of the muscle and apparently contributes a few fibers upwards into the main semispinalis-spinalis complex.

M. Longissimus Dorsi (ML)

The longissimus in *Xenopeltis* arises from a well developed tendon attached to the ventro-anterior surface of the prezygapophysial buttress. From this point the long flat muscle extends cranio-medially to divide at about the level of the fourth vertebra. The medial, or dorsal portion continues cranially and medially to insert in a normal fashion on the postero-lateral portion of the neural spine of the ninth vertebra cranial to the point of origin. The lateral belly is continued as a tendon antero-ventrally to eventually become the origin of the medial belly of the retractor costae. At the point of origin of the longissimus a well developed tendon runs ventro-cranially to insert on the rib of the next vertebra anteriorly. A similar attachment is found in *Sanzina*, though it occurs much more anteriorly to the origin of the longissimus.

M. Multifidus (MM)

The multifidus in *Xenopeltis* seems to be normal, arising from a tendinous arch and extending anteriorly to insert into the caudal border of the neural arch of a vertebra three segments anteriorly.

M. Interarticularis Superior (IAS)

This muscle is small, simple, and normal for the boid condition, extending from one postzygapophysial process to the same process on the next vertebra anteriorly.

The transversus dorsalis, costovertebrocostalis, retractor costae, costalis internis superior and interarticularis inferior all seem normal.

The most significant columnar variation beyond that described for *Sanzina* (Auffenberg, 1958) is that the complexity of the semispinalis and spinalis in the anterior and middle of the body is not found posteriorly. In this region each tendinous arch seems to give rise to a separate fused unit of semispinalis and spinalis, and adjacent arches do not contribute fibers to the main belly.

DISCUSSION

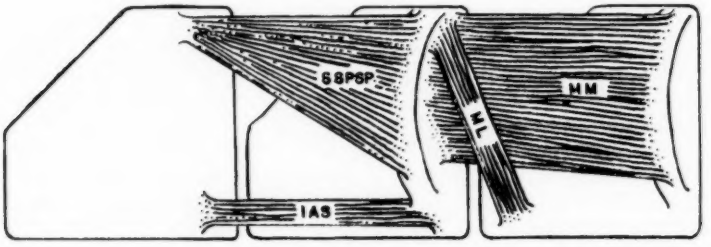
The exact phyletic positions of most of the snakes discussed are not clear and the present myological study sheds little light on this problem. Deviations in muscular arrangement are in some cases suggestive of intermediacy between typical boines (such as *Constrictor*) and the Colubridae (as represented by *Coluber*). However, this intermediacy is not interpreted as having important phyletic significance; but rather, seems indicative of some degree of parallel, or convergent, evolution. Thus, it is suggested that a number of boid or boid-like groups have independently evolved colubrid-like myological modifications several times in the past. This phenomenon in its variety of

forms is here termed "myological colubridization." A similar situation regarding certain osteological characters of boid, and boid-like forms, has been intimated by Dowling (1959).

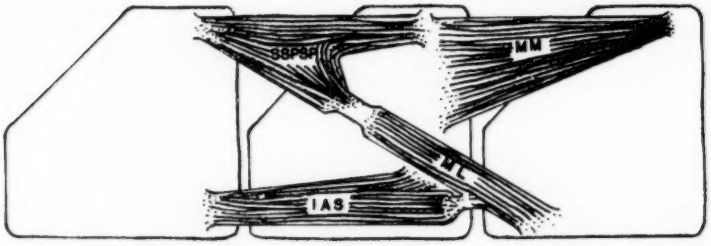
There are two major tendencies indicated in the evolution of more complex from simpler, presumably more primitive, myological types. These are: (1) the tendency for median myological elements to become associated with more lateral ones, and (2) a tendency for anterior elements to become morphologically associated with more posterior ones, thereby lengthening considerably certain functional units through fusion of shorter muscles (Fig. 1.).

In a more detailed fashion, the major trends in the evolution of trunk musculature are here believed to include the following:

1. Abandonment of the tendinous arch as a point of origin by the semispinalis and/or the spinalis and the multifidus.
2. Association of the interarticularis superior with other myological elements through the interlacing of fibers, or by tendinous asso-



PRIMITIVE BOID



ADVANCED COLUBRID

Fig. 1.—Diagrammatic lateral view of primitive and advanced myological types, showing the loss of tendinous arches, migration of the longissimus, and splitting of the spinalis and superior interarticularis complexes in the more advanced condition.

ciations. Primitively this association is with the spinalis complex, or with the multifidus. In advanced forms it is with the longissimus.

3. Splitting of the interarticularis superior posteriorly (forming the digastricus in its variety of forms in some boids, boid-like groups, and other families of snakes).

4. Splitting of the spinalis complex into two muscles, the semispinalis and spinalis. This fission apparently takes place posteriorly in its initial phases, and becomes complete with the cranial migration of the cleft.

5. Association of the semispinalis with other myological units through the interlacing of fibers or by tendinous associations. Primitively this association is with the interarticularis superior. In more advanced forms it is with the multifidus or especially the longissimus.

6. Association of the longissimus with other muscles through the interlacing of fibers or by tendinous associations, such as with the semispinalis, or the interarticularis superior.

7. Loss of osseous insertion of the longissimus.

8. Lengthening of muscle segments through loss of osseous attachments and an increase of interlacing fibers between identical metameric myological segments.

One or more of these trends are seen in many of the boid and boid-like forms. Of the genera examined, the most common modification is one in which the interarticularis superior is associated with a more dorso-medial muscle. This association is usually with the semispinalis, or the semispinalis portion of the spinalis complex if the latter is fused (*Sanzina, Eryx, Calabaria,* and in a somewhat modified form in *Anilius*). With the exception of *Anilius*, the advanced colubrid condition (association with the longissimus dorsi) has not been recognized in any boid, or boid-like family. In *Anilius* the association is in the form of a common osseous areal origin for both muscles, while in the Colubridae the origin of the interarticularis superior is on the longissimus itself. *Tropidophis* exhibits a singular case in which the association of the interarticularis superior is with the multifidus.

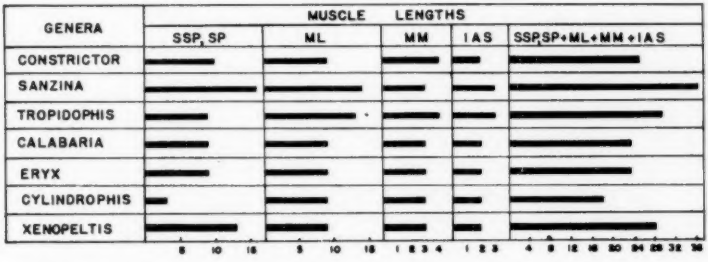


Fig. 2.—Comparative thoracic muscle lengths in various boid, and boid-like snakes

The next most common trends are the division of the spinalis and semispinalis, and the lengthening of particular muscles to cover a greater number of vertebrae. Division of the spinalis complex provides for individual action of two myological units rather than one, in which one of the units is more lateral in action than the other. In the more primitive condition the origin of the spinalis and semispinalis remains on the tendinous arch (*Cylindrophis*). In more advanced types either the origin of the spinalis *or* semispinalis portions is off of the arch (*Anilius, Tropidophis* and *Eryx*). Only in the Colubridae do both muscles lack the arch as a point of origin.

Comparative lengths of the muscle units in genera examined is shown in Figure 2. From these illustrations it is seen that the longissimus, interarticularis superior, and multifidus seem most stable. The spinalis complex is most variable.

The genera also differ in the degree of elongation of any particular muscle. Thus, *Sanzina* possesses the longest spinalis and longissiimus muscles; *Constrictor* and *Tropidophis* the longest multifidus, and *Tropidophis* the longest interarticularis superior. Within a single genus comparisons of another type are possible. Thus, *Xenopeltis* possesses a long spinalis complex, but is normal in other units considered; *Cylindrophis* possesses the shortest spinalis complex, but is normal in other units considered; *Eryx* is conservative in all of the units studied, etc.

A comparison of the total length of all myological elements considered important in this study (SSP, SP + ML + MM +IAS) (Fig. 2) shows that of the boid and boid-like genera examined, *Sanzina* has the greatest accumulative length, then *Tropidophis, Xenopeltis* and *Constrictor* in respective decreasing lengths. The totals for *Calabaria* and *Eryx* are rather small. *Cylindrophis* has the shortest accumulative length of all.

The next trends in decreasing order of abundance are the associative nature of the spinalis with some other myological element, and the abandonment of the tendinous arch as a point of origin for the multifidus.

Association of the spinalis complex with the interarticularis superior by means of interlacing fibers has been discussed above. In *Anilius* the spinalis is associated with the interarticularis superior by a common areal origin, and with the longissimus by a connecting tendon. In *Xenopeltis* each segment of the spinalis complex is associated with two preceding and one succeeding unit through the interlacing of spinalis fibers originating from the tendinous arches of these vertebrae. In *Coluber* the spinalis arises at the point of origin of the longissimus, a condition approached only by *Anilius* among the boid and boid-like forms examined so far.

The loss of the tendinous arch as an attachment for the multifidus is found in *Anilius* and *Calabaria*. In *Anilius* the fibers originate on the dorsal surface of the neural arch, as they do in the Colubridae. In *Calabaria* the origin of the muscle is unique in that it is not on the arch, but on the cranio-lateral portion of a neural spine.

Two other trends of equal occurrence are the posterior division of the interarticularis superior to form the digastricus, and the abandonment of the tendinous arch as a point of origin for only one of the two members of the spinalis complex.

Among boid and boid-like forms a posterior division of the interarticularis superior is found in *Anilius, Eryx* and *Tropidophis*. Mosauer (1938) considered such a condition a colubrid character. The interlacing of the fibers of the interarticularis superior and the spinalis complex (*Sanzina* and *Calabaria*) is here interpreted as a condition leading to the formation of a digastricus, since if these connecting fibers became more numerous and longer a 'Y' or 'V'-shaped muscle would be produced. The condition found in *Cylindrophis*, where a long, thin tendon associated with the semispinalis sends a small slip into the interarticularis superior is apparently unique. In this case the tendon may represent a part of the interarticularis superior that had migrated dorsally and become almost completely separated from the functionally important lower and larger unit.

The semispinalis abandons the tendinous arch in *Anilius*, where the muscle has apparently moved laterally. In *Eryx* the spinalis has moved medially to originate completely on the neural spine. The myological arrangement in the latter is thus similar to that in the Colubridae where the spinalis extends from neural spine to neural spine. However, as far as is known all colubrid snakes completely lack the tendinous arch.

The most uncommon of the trends in myological colubridization among the forms examined is an association of the longissimus with some other unit. In the Colubridae this association is (at the origin of the longissimus) with the spinalis, and (near its insertion) with the interarticularis superior. This condition is apparently approached (in a modified fashion) in the genus *Anilius*, where the muscle is associated with both the semispinalis and the interarticularis superior. However, in this genus the insertion of the longissimus is still on a prezygapophysis, whereas in the Colubridae the insertion is not on a bony element at all, but is continuous with the spinalis. The loss of an osseous insertion for the longissimus and the complete abandonment (and absence) of a tendinous arch by the spinalis and semispinalis are characters not known to occur in the Boidae, or in any closely related groups. Both features apparently represent a culmination in myological modifications, some of which are found in lower phyletic units.

Figure 3 is a diagramatic illustration of the nature of each of the major myological units discussed so far. Of particular importance are the cases of modifications paralleling those found in the Colubridae. Some of these are: the association between medial and lateroposterior muscles, lengthening of individual myological units, and migration and loss of various types. The probably independent formation of a partially divided interarticularis superior in *Anilius*, *Tropidophis* and *Eryx* (and in a less advanced condition, the simple association of the interarticularis superior and the spinalis complex

in several genera); lengthening of specific muscle segments; loss of the tendinous arch as an origin for the multifidus and/or the spinalis complex, are all considered to be modifications in response to a general tendency to increase efficiency in movement. They seem to have little, if any, phyletic basis. Several degrees and types of modification may be found within a presumable closely related series of genera. The same is true in an analysis in which myological arrangements

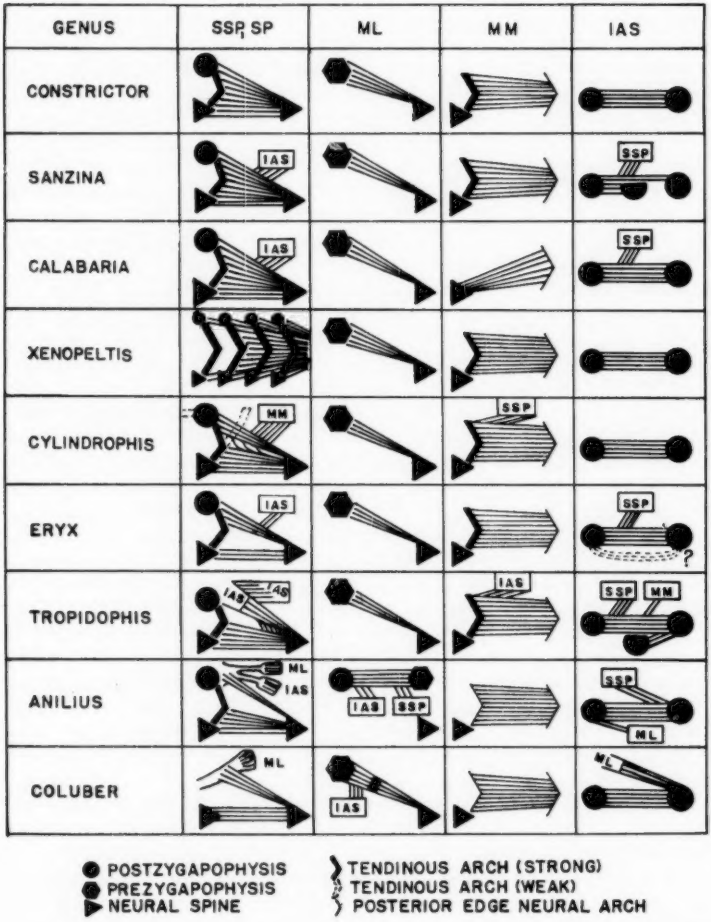


Fig. 3.—Diagrammatic representation of the origins, insertions and myological associations of each of the major epaxial thoracic muscles in the genera studied.

are compared with general shape or modes of existence. However, certain minor modifications are associated with type of activity. Thus, in most fossorial snakes the more dorsal muscle units have as their origin and insertion areas proportionately closer to the longitudinal axis of the centrum than do surface dwelling forms. This is well illustrated in the lower neural spines and neural arches of almost all fossorial snakes. In most of these genera the spinalis complex and multifidus are reduced in dorso-ventral thickness. Both of these units are concerned with moving more anterior parts of the body dorsally and laterally. On the other hand, fossorial snakes seem to have better developed longissimus and interarticularis complexes. These muscles are presumably largely involved with lateral movements. In arboreal forms, or at least forms showing some proficiency in an arboreal habitat, where vertical movements of the body are more commonly necessary for efficient progression, the spinalis complex and multifidus are well developed. The neural spines and arches are relatively higher. The lateral members of the epaxial musculature may, or may not be more well-developed.

Figure 4 illustrates the hypothetical evolutionary steps from the much simpler basic boid type of that found in the colubrids. The major steps seem to be (A) association of the interarticularis superior with the fused spinalis complex; (B) separation of the spinalis complex into semispinalis and spinalis; (E) lengthening and anterior migration of the associative fibers of the articularis superior; (F) posterior migration of the longissimus along the semispinalis; loss of the tendinous arch; and, (G) loss of an osseous origin for the semispinalis. No actual examples of certain arrangements have yet been found (steps B, C and D), though very similar conditions have been observed. It is assumed that these slightly modified versions passed through the more basic hypothetical steps. It is quite possible that myological studies on other boid and boid-like forms will disclose arrangements representing these missing stages.

Forms such as *Eryx, Tropidophis, Xenopeltis, Cylindrophis* and *Anilius* seem to represent independently modified arrangements which evolved from the more basic types. Thus, *Cylindrophis* and *Eryx* are approximately at the same level of myological colubridization, since both possess a rather simple arrangement, but with a split spinalis complex (hypothetical step B). However, each genus has taken this arrangement one step further by losing the tendinous arch as a point of origin for one of the two muscles in the complex. In *Cylindrophis* the semispinalis obtains an osseous origin, while in *Eryx* the spinalis does. *Tropidophis* and *Anilius* are also basically at the same level in that they both possess separate semispinalis and spinalis units; possess a tendinous arch; only the spinalis has its origin completely on the arch, and both have a well developed bipartate interarticularis superior, with the origin for the medial belly being well forward (hypothetical step E). However, they are also quite different. In *Tropidophis* the *multifidus* is associated with the interarticularis superior, which in turn spans two vertebrae, rather than one.

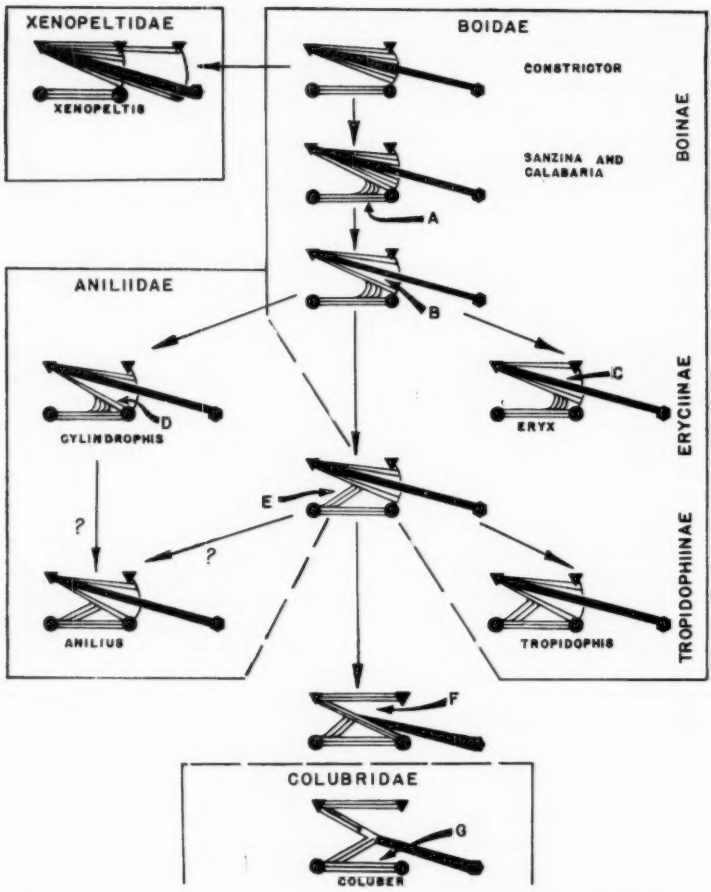


Fig. 4.—Hypothetical evolutionary steps from the simple basic boid type to that found in the colubrids. The major steps are: A, association of the interarticularis superior with the fused spinalis complex; B, separation of the spinalis complex into semispinalis and spinalis; E, lengthening and anterior migration of the associative fibers of the interarticularis superior; F, posterior migration of the longissimus along the semispinalis and loss of a tendinous arch; G, loss of an osseous origin for the semispinalis. Steps C and D are parallel developments in which one member of the spinalis complex has migrated off of the tendinous arch. Steps B, E and F are hypothetical, since no genera have yet been studied which exhibit any of these patterns. *Xenopeltis, Cylindrophis, Anilius, Eryx* and *Tropidophis* all illustrate myological arrangements which, in some form or another, parallel the hypothetical evolutionary steps leading to the colubrid condition. Symbols the same as in Figure 3.

In addition, the arrangement in *Anilius* is much more advanced in degree. The two forms are not necessarily closely related. Both arrangements could have evolved from hypothetical step E, or, more likely, *Tropidophis* from step E and *Anilius* from a *Cylindrophis*-like arrangement (D), in which the origin of the associative fibers of the interarticularis superior had simply migrated anteriorly.

Xenopeltis represents a slightly modified primitive pattern, apparently not on any line leading to higher types. *Sanzina* and *Calabaria* are both very close to step A, and perhaps quite close to the line leading to higher types.

When a logical scheme of classification (Dowling, 1959) for these forms is superimposed on this illustration of hypothetical steps in the evolution of trunk musculature, an interesting series of speculative taxonomic considerations becomes evident. Some of these are of interest in regard to possible phyletic arrangements. Thus, *Tropidophis* and *Eryx* can only be considered boids if steps B and E are present in boids. If *Loxocemus* is found to have a pattern identical, or close, to step B this genus should be placed in the Boidae, unless the Eryciinae and/or the Tropidophiinae are to be raised to familial standing. On the other hand, if *Loxocemus* is considered a member of the Aniliidae and the musculature is similar, or identical to that in step E, the Tropidophiinae would have to be raised to familial status. In this event the relationship of *Cylindophis* and *Anilius* become obscure.

Much remains to be learned regarding the relationships of many groups of snakes. Myological studies of broader type may shed considerable light on some of these problems, though it should not be envisioned that such studies will provide all the answers. In some respects such data may raise more questions than they answer. Several additional genera of anilids and the genus *Loxocemus* (regardless of its current or future placement) should be examined in an attempt to clarify questions raised by this study. Also important would be myological study of typhlopid and leptotyphlopid genera. Of advantage would be a study of the musculature of the more primitive colubrid genera. Some of these may be found to possess a musculature identical to the presently hypothetical step E. More important, such a study would lay the foundation for a more exhaustive examination of more specialized arrangements in the family Colubridae, some of which are suggested in Mosauer's survey and others in observed vertebral peculiarities necessitating modifications of some sort. A pilot study of the trunk musculature of several genera of lizards utilizing different methods of progression above and below the surface of the ground may be quite useful. Parallel myological modifications in limbless lizards and snakes might be sought with profit.

All of these studies, pursued in a systematic and co-ordinated fashion, would contribute greatly to our knowledge of the relationships and functional morphology of the snakes. There is a great need for analysis of all kinds of characters on a generic and supergeneric level. Perhaps altogether too much emphasis is currently

being placed on external characters useful in analysis of geographic variation, with the definition of subspecific categories being an end in itself. Such variational studies are useful and important. However, in North America the patterns of geographic variation in snakes are fairly well established, and the information on a large number of species and generic analyses need only be drawn together to provide a more timely and significant statement regarding the nature of the patterns and the reasons for noncoincidence or coincidence.

REFERENCES

AUFFENBERG, W. 1958. The trunk musculature of *Sanzina* and its bearing on certain aspects of the myological evolution of snakes. *Breviora*, **82**: 1-12.

BELLAIRS, A. D'A., AND GARTH UNDERWOOD 1951. The origin of snakes. *Biol. Rev. Cambridge Philos. Soc.*, **26**: 193-237.

DOWLING, H. G. 1959. Classification of the Serpentes: a critical review. *Copeia*, **1959**: 38-52.

MOSAUR, W. 1935. The myology of the trunk region of snakes and its significance for ophididian taxonomy and phylogeny. *Publ. Univ. Calif. Los Angeles*, **1**: 81-120.

ROMER, A. S. 1956. *Osteology of the Reptiles*. Univ. of Chicago Press, Chicago. i-xxi, 1-772 pp.

The Live Oaks of the Series Virentes

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ABSTRACT: Key and descriptions of the 6 species and 1 variety are illustrated, distinctions being based upon morphological, geographic, and ecological (soil tolerance) data. New dispositions include *Quercus minima* Small X *Q. chapmani* Sarg. (= *Q. rolfsii* Small), *Q. hemispherica* var. **maritima** (= *Q. phellos* β *maritima* Michx. — not *Q. virginiana* var. *maritima* Sarg., a misidentification), *Q. virginiana* Mill. (= *Q. oleoides* var. *quaterna* C. H. Mull.), and *Q. oleoides* var. **sagraeana** (= *Q. sagraeana* Nutt.).

The series *Virentes* of *Quercus* comprises an aberrant natural group within the subgenus *Lepidobalanus*. Typified by *Quercus virginiana*, this small group has come to be known as the "southern live oaks" by reason of its concentration in the southeastern United States and by contrast with the many evergreen species of unrelated series in the southwestern United States, on the coast of California, and in Mexico.

The species of *Virentes* occurring in the United States have, since their original proposals, been given two significantly different treatments. The less conservative treatment of Small (1913, 1933) credits six species to this area, while Sargent (1918) reduces such of these as he treated to the status of varieties under *Quercus virginiana*, simultaneously proposing additional varieties based upon less profound differences. Since neither of these authors concerned himself with the Latin American members of the series, the group has not yet been critically reviewed as a whole. The treatment accorded it by Trelease (1924) incorporated a compromise of Sargent's and Small's views with relatively minor additional modification. In evaluating Trelease's monograph, it must be remembered that he originally set out to do the Latin American species only and that he extended his treatment to the entire North American continent largely by incorporating the treatments of Sargent in the eastern United States and Rydberg in the western United States, subjecting neither to very critical analysis.

The present treatment[1] is motivated by the necessity of a review of the series in preparation for the statement of some evolutionary conclusions to which field and herbarium studies have led me. Although I readily admit the provisional character of some of the conclusions here presented, there are included some geographic, ecological, and morphological evidences of genetic relations (and genetic distinctions) not

[1] I am indebted to the Associates in Tropical Biogeography and the Faculty Committee on Research, both of the University of California, for financial aid in prosecuting the field studies and to the National Science Foundation (project G-2713) for support of both field and herbarium studies upon which this work is based.

heretofore emphasized. An exhaustive field study of the *Virentes* in the southeastern United States, Cuba, and Mexico was initiated, but its continuation would undoubtedly go far toward a satisfactory solution of the problems posed by such plants as the one here called *Quercus virginiana* (juvenile). On the other hand, available ecological descriptions (e.g., Harper, 1913, 1914, 1915, 1927, 1928) have proved, upon checking in the field, to be invaluable in explaining the continued maintenance of *Q. virginiana, Q. geminata,* and *Q. minima.* In the course of wide reading in the voluminous ecological literature on the Southeastern Coastal Plain, I was able to find sizable quantities of useful information only in Harper's extensive writings. These works are to be commended to taxonomists and ecologists alike as rich sources of information on the distribution of species and vegetation types in relation to topography and soils, all the more valuable because of their singular freedom from philosophic "isms" and consequent theoretical bias.

Unlike some of the other natural groups in Quercus, there is no evidence that the series *Virentes* has been enriched to any great degree by hybridization with the species of other series. Such outcrossing does occur, but it does not result in significant hybrid swarms nor in any important degree of introgression. Hybridization within the series, on the other hand, has had much more tangible results and is to be made the subject of a separate paper in the near future. The natural hybrids involving species of *Virentes* as one or both parents are not here treated exhaustively, although the occurrence of intergrades of hybrid origin is noted where these are of importance to the present study or to the projected evolutionary discussion.

Quercus series *Virentes* Trel., *Mem. Nat. Acad. Sci.* 20:112. 1924.

Dryopsila Raf., *Alsogr. Am.* 25. 1838. (*pro parte*).
Quercus subgen. *Finax* Raf. *Alsogr. Am.* 28. 1838.
Quercus [sect.] *Virginianae* Small, *Man. S.E. Flora* 422. 1933.

Large trees to low rhizomatous shrubs. Bark dark brown or black and deeply furrowed, smooth and hard on vigorous young trunks and branches. Twigs minutely fulvous-stellate-tomentulose (or with glandular puberulence and spreading hairs admixed). Buds rounded, nearly glabrous, usually russet. Leaves evergreen, coriaceous or chartaceous, often quite thick, small or moderate-sized, predominantly elliptic and subentire or obovate and repandly coarse-toothed, margins slightly or very markedly revolute, blades plane or strongly concave beneath, glabrous or nearly so and lustrous above, minutely appressed-stellate-canescent beneath, sometimes with spreading stellate hairs and glandular puberulum in addition; veins highly reticulate, moderately or very prominent beneath or relatively obscure, sometimes impressed above. Staminate catkins stellate-pubescent, the pubescent anthers moderately exserted from the calyces. Fruit annual, moderate-sized, the cups characteristically turbinate, the scales canescent or fulvous.

Range.—Southern Atlantic United States and Cuba to Central West

Texas, Coahuila, and Baja California, and southward along the Gulf of Mexico to Costa Rica.

Type.—*Q. virginiana* Mill.

KEY TO SPECIES AND VARIETIES

1. Leaves with veins markedly impressed above, very prominent beneath, lower surface with prominently spreading hairs.
   2. Leaves markedly concave beneath, plants of the southeastern United States ..... 5. *Q. geminata.*
   2. Leaves plane or only slightly concave beneath, plants of Cuba ..... 6a. *Q. oleoides* var. *sagraeana.*
1. Leaves with veins slightly or not at all impressed above, obscure or only moderately prominent beneath, lower surface with appressed minute stellate tomentulum and at most scattered spreading hairs.
   3. Leaves predominantly broadly rounded apically, the blades broadest above the middle
      4. Low rhizomatous shrubs.
         5. Leaves densely appressed-stellate-tomentulose beneath.
            6. Leaves basally cuneate, usually dimorphic, the upper narrowly oblong and usually entire, the lower broadly obovate and coarsely toothed ..... 4. *Q. minima.*
            6. Leaves rounded or obtuse at base, various but not dimorphic as above ..... 1. *Q. virginiana* (juvenile).
         5. Leaves sparingly appressed-stellate beneath or at length glabrate ..... 4a. *Q. minima* x *Q. chapmani.*
      4. Trees or at least large shrubs 3 m tall.
         7. Leaves normally three times as long as broad, plants of the southeastern United States ..... 1. *Q. virginiana.*
         7. Leaves not over twice as long as broad, plants of the Gulf Coastal Plain of Mexico and Central America ..... 6. *Q. oleoides.*
   3. Leaves predominantly acute, the blades broadest below the middle.
      8. Acorns markedly fusiform, over three times as long as broad, plants of the Cape Region of Baja California ..... 3. *Q. brandegei.*
      8. Acorns not as much as three times as long as broad.
         9. Acorns barrel-shaped, not twice as long as broad, plants of the Gulf and Atlantic Coast of the United States.
            10. Shrubs ..... 1. *Q. virginiana* (juvenile).
            10. Trees ..... 1. *Q. virginiana.*
         9. Acorns subfusiform, often twice as long as broad, plants of the piedmont in the Edwards Plateau of Texas and the Sierra Madre Oriental of Mexico ..... 2. *Q. fusiformis.*

1. *Quercus virginiana* Mill., *Gard. Dict.*, ed. 8, no. 16. 1768.

   Q. sempervirens Walt., *Fl. Carol.* 234. 1788.
   Q. virens Sol. in Ait. *Hort. Kew.* 3:356. 1789.
   Q. andromeda Riddell, *New Orleans Med. & Surg. Jour.* 9:614. 1853.
   Q. virginiana var. *virescens* Sarg., *Bot. Gaz.* 65:446. 1918.
   Q. virginiana var. *eximea* Sarg., *Bot. Gaz.* 65:447. 1918.
   Q. eximea Trel., *Mem. Nat. Acad. Sci.* 20:116. 1924. (*nom. prov.*).
   Q. andromeda f. *nana* Trel., *Mem. Nat. Acad. Sci.* 20:116. 1924.
   Q. oleoides var *quaterna* C. H. Mull., *Contr. Texas Research Found.* 1:76. 1951. (*pro max. parte, typus excl.*).

Moderate to very large trees with broad spreading crowns and roughly furrowed brown or black bark or maturing as low rhizomatous shrubs less than 1 m tall. Twigs 1.5 to 3 mm thick, densely or sparsely gray- or fulvous-tomentulose with a mixture of appressed stellate and glandular hairs and waxy puberulum, the second season gray and nearly glabrate or usually persistently pubescent. Buds 1.5 to 3 mm long, subglobose or rounded-quadrangular, glossy dark red and glabrous or sparingly puberulent; stipules 2 to 4 mm long, subulate, sparsely pubescent, soon caducous. Leaves evergreen or subevergreen, hard and coriaceous, rather thick or moderately thin, 1 to 15 (usually 3 to 10) cm long, 0.3 to 3 or 4 cm broad, oblong or oblanceolate to obovate, predominantly broadest above the middle, broadly rounded or acute in juvenile forms, cuneate or sometimes rounded basally, entire or coarsely and irregularly few-toothed, especially in juvenile forms, margins nearly plane or minutely revolute, blade flat or (especially in thicker forms) slightly concave beneath, upper surface glossy and glabrous or sparingly stellate-pubescent especially about the base of the midrib, lower surface dull, canescent or green, densely covered with minute appressed-stellate hairs on waxy puberulum, or very sparsely pubescent in the green form, midrib and veins usually glabrous; veins about 7 to 11 on each side and with occasional intermediates, irregularly branching and obviously anastomosing, somewhat prominent above and below or rather obscure. Petioles 1 to 10 mm long, densely or moderately stellate-tomentulose. Staminate catkins 1.5 to 5 cm long, the sparsely tomentose peduncle rather loosely flowered, the pubescent anthers moderately exserted from the variously pubescent calyx. Pistillate catkins 1 to 4.5 cm long, 2-or 3-flowered distally on the tomentulose peduncle. Fruit solitary or paired on a coarse peduncle 0.5 to 2 or more cm long; cups 8 to 12 mm high, 9 to 15 mm broad, hemispheric to deeply goblet-shaped, usually markedly constricted basally, the scales markedly thickened basally, densely white or silvery tomentulose, the apices dark red and glabrous or puberulent; acorns 15 to 22 mm long, 9 to 15 mm broad, narrowly or broadly barrel-shaped, apex always rounded, glabrous and glossy brown or with a waxy glaucous bloom, about one-third included.

Range.—Coastal plain, immediately adjacent to the coast, Virginia to Florida and west to Texas, inland only at the low elevations of peninsular Florida and locally on old beach lines in Louisiana and Georgia.

Quercus virginiana is the largest, most widely spread, and most abundant species of the series and is therefore easily the most prominent. It rarely extends above the coastal prairie and is confined largely to moderately heavy soils, or gravelly soils containing clay, in the immediate vicinity of the coast. It is absent from deep, relatively pure sand over nearly all of its range, its place being taken there by related species. The one exception noted (on the sand dunes of Brooks and Kenedy Counties, Texas) remains unexplained, unless it relates to hybrid influence by *Q. oleoides*. Where the species approaches piedmont topography (e.g., the limestone areas of the Edwards Plateau of

Texas) it is replaced by *Q. fusiformis* with which it intergrades on sites variously intermediate in character between the immediate coast and the inland uplands on which *Q. fusiformis* grows. Outlying limestone outcrops and clay beds on the Coastal Plain in Atascosa, DeWitt, Goliad, and Victoria Counties in Texas harbor true *Q. fusiformis*.

The exact nature of the form referred to *Quercus virginiana* (juvenile) is obscure, for it merges with the species both geographically and ontogenetically while still suggesting some genetic distinctness. The form, like the species, occurs on heavy soil and is confined to the immediate coastal areas. As described in a previous paper (Muller 1951a), *Q. virginiana* develops into a rhizomatous shrub, a form which it maintains indefinitely before assuming tree form. In a pure population of the species the fruiting shrub stage occurs mixed with the mature trees and all gradations between are in evidence. It is my opinion that there exists no genetic difference responsible for the two fruiting forms and that this is not deserving of varietal distinction. The shrub form is therefore treated here as a "juvenile" form of *Q. virginiana*.

Some part of the distinction suggested may result from the influence of hybridization of *Quercus virginiana* with *Q. oleoides*. A few characters of *Q. oleoides* are visible in the extreme southwestern coastal population of *Q. fusiformis* in Texas as well as in some adjacent populations of *Q. virginiana* (described as *Q. oleoides* var. *quaterna*). A recent extensive field study in the northernmost coastal populations of *Q. oleoides* in Tamaulipas failed to reveal a close relationship of that species to the proposed Texan variety. Thus, the southwestern extremity of *Q. virginiana* clearly carries a few characters of *Q. oleoides*, but scarcely enough to prejudice its reference to *Q. virginiana*. Its essential identity with the Atlantic coastal tree and shrubby forms requires the entire assemblage to bear the name here applied. This problem is discussed more fully under the next species following.

Specimens examined:

VIRGINIA: Norfolk Co., *M. D. Blanchard s. n.; N. L. Britton s. n.* (*pro parte*, cf. also *Q. minima*); *F. V. Coville* 19; *T. H. Kearney Jr.* 1215, 1224, 1450, 1754; Northampton Co., *M. L. Fernald, B. Long* and *J. M. Fogg Jr.* 5292; Princess Ann Co., *A. Chase* 2347; *J. R. Churchill s. n.; M. G. Henry* 2577; *L. Hubricht* B2364; *E. C. Leonard* and *E. P. Killip* 271, 289a; *C. D. Mell s. n.;* York Co., *J. W. Chickering s.n.; H. W. Henshaw s. n.; Hollick* and *N. L. Britton s. n.* (*pro parte*, cf. also *Q. fusiformis*); *C. H. Merriam s. n.; T. Morong s. n.; C. H. Muller* 10353; *W. M. Rankin s. n.; J. Schneck s. n.; G. Vasey s. n.; L. F. Ward s. n.*

NORTH CAROLINA: Brunswick Co., *W. W. Ashe s.n.; V. H. Chase s. n.; F. V. Coville* 132; Cartaret Co., *R. K. Godfrey* 6387; Dare Co., *W. W. Ashe s. n.; W. R. Maxon* 10611; New Hanover Co., *H. H. Bartlett* 2549; *W. H. Canby s. n.; R. K. Godfrey* 4840; *G. McCarthy s. n.;* County undetermined, *M. Curtis s. n.; J. A. Harris* 19558.

SOUTH CAROLINA: Beaufort Co., *T. G. Harbison* 3533; *J. A. Harris* 19714; *J. H. Mellichamp s. n.; C. H. Muller* 9939; *C. S. Sargent s. n.;* Berkeley Co., *R. K. Godfrey* and *R. M. Tryon Jr.* 1612; Charleston Co., *K.*

W. Hunt 419d, 521f, 547c, 2668, 3356, 3358; *H. N. Moldenke* 5170 (*pro parte*, cf. also *Q. pumila* and *Q. minima*), 5174; *J. Schneck s. n.; J. K. Small s. n.; J. K. Small* and *L. M. Bragg s. n.;* Chesterfield Co., *A. E. Radford* 9123; Florence Co., *J. L. Seal* 7; Georgetown Co., *R. K. Godfrey* and *R. M. Tryon Jr.* 1092; *C. H. Muller* 3861, 3862, 3864, 3864a, 3864b; Jasper Co., *C. P. Alexander* 286; *C. Mohr s. n.; C. S. Sargent s. n.;* Lexington Co., *E. A. McGregor* 202, 238, 239, 636; Orangeburg Co., *W. W. Eggleston* 4947, 4948; County undetermined, *J. A. Harris* 2140; *J. H. Mellichamp s. n.*

GEORGIA: Camden Co., *C. H. Muller* 10463; Chatham Co., *R. M. Harper* 725; Dougherty Co., *C. Orr* 1, 1a, 1b; Glynn Co., *C. H. Muller* 9921; Lee Co., *W. H. Duncan* 3093; *R. M. Harper* 1151; Liberty Co., *T. G. Harbison* 27; Thomas Co., *E. Eggleston s. n.; J. K. Small s. n.;* County undetermined, *Brendel s. n.; J. B. Jones s. n.*

FLORIDA: Alachua Co., *T. G. Harbison* 5344; *W. A. Murrill* 180, 472; Brevard Co., *Bates s. n.; A. B. Burgess* 622; *A. S. Rhoads* 8395; Broward Co., *W. C. Coker s. n.;* Charlotte Co., *Blodgett s. n.;* Clay Co., *T. G. Harbison* 16293 and/or 7048; Collier Co., *J. K. Small* and *J. P. Dewinkeler* 9925; Dade Co., *E. A. Bessey* 17, 85; *N. L. Britton* 99; *N. C. Cowles s. n.; H. N. Moldenke* 5465, 5512, 5854; *M. F. Moseley* 377, 378, 379, 380, 381, 382, 383, 386; *C. A. Mosier* 349, 353, *s. n.; C. A. Mosier* and *W. E. Stafford* 61, 62, 76, 77; *W. E. Stafford s. n.; J. K. Small* 7255, 8073, 8074, *A; J. K. Small* and *J. J. Carter* 1318, 2482; *J. K. Small* and *G. V. Nash* 69, *s. n.; J. K. Small, J. W. Small* and *J. P. DeWinkeler* 10326, 10326a, *s. n.; A. Rehder* 818; *J. P. Young* 230; DeSoto Co., *C. H. Muller* 9833; Dixie Co., *T. G. Harbison* 69; *C. H. Muller* 9824; Duval Co., *D. Demaree* 20750; Flagler Co., *C. H. Muller* 9905; Franklin Co., *A. W. Chapman s. n.; C. H. Muller* 9804, 10261; Gadsen Co., *T. G. Harbison* 3671; Gulf Co., *W. L. McAtee* 1770b; *C. H. Muller* 9801; Hernando Co., *R. N. Jones* 140; Highlands Co., *A. H. Howell* 1072; *J. P. McFarlin* 8432, 8432a; Hillsborough Co., *A. P. Garber s. n.;* Jefferson Co., *C. H. Lighthipe s. n.;* Lafayette Co., *T. G. Harbison* 5565; Lake Co., *Bosanquet s. n.; G. V. Nash* 1693; Lee Co., *J. P. Standley* 225; *P. C. Standley* 12776, 52574; Leon Co., *J. H. Beal s. n.; N. K. Berg s. n.; C. H. Muller* 10471; *E. J. Palmer* 35228, 35231; *Reese* 628, 629, 630, 631, 632; *F. Rugel s. n.; A. Steward s. n.;* Levy Co., *T. G. Harbison* 3177; *Reese* 750; Manatee Co., *A. P. Garber s. n.; J. H. Simpson* 11, 65, *s. n.;* Marion Co., *C. D. Mell s. n.; C. H. Muller* 9830; *L. F. Ward* and *R. Ward s. n.;* Martin Co., *C. H. Muller* 9879; Okeechobee Co., *J. K. Small, E. G. Britton, N. L. Britton* and *J. P. DeWinkeler* 925a; *Orange Co., F. S. Blanton* 6488, 6543; *J. G. Grossenbacher s. n.; M. Meislahn* 42; *H. O'Neill s. n.;* Osceola Co., *E. A. Mearns s. n.;* Putnam Co., *G. Smith* 7617, *s. n.;* Santa Rosa Co., *C. H. Muller* 9780; Seminole Co., *T. G. Harbison s. n.; A. P. Garber s. n.; H. O'Neill s. n.; S. Rapp* 3, 9, 9a, 14, *s. n.;* St. Johns Co., *A. Chase* 7016; *J. A. Harris* 21194; *J. K. Small* and *J. J. Carter* 1441; Taylor Co., *C. H. Muller* 9818, 9819, 9820, 9821; Volusia Co., *A. B. Burgess* 610; *C. H. Muller* 9895; Walton Co., *C. H. Muller* 9784, 9786; Wakulla Co., *J. H. Beal s. n.; R. K. Godfrey* and *R. Kral* 53921; *C. H. Muller* 9814; *Reese* 627; *F. Rugel s. n.;* County undetermined, *Beyrich s. n.; W. H. Canby s. n.; A. W. Chapman s. n.; Manigault s. n.; W. L. McAtee s. n.; W. E. Stafford* 1763.

ALABAMA: Baldwin Co., *C. H. Muller* 9779; Mobile Co., *H. H. Bartlett* 3210; *J. M. Bigelow s. n.; B. F. Bush* 218; *D. Demaree* 35104; *C. Mohr s. n.; J. Schneck s. n.; Van Aller* 1.

MISSISSIPPI: Coahoma Co., *J. L. Alcom s. n.;* George Co., *D. Demaree* 34039; *C. H. Muller* 9974; Hancock Co., *C. H. Muller* 9763; Harrison Co., *A. Dachnowski-Stokes s. n.; T. G. Harbison* 3657, 3658; *J. F. Joor s. n.;*

C. H. Muller 10008; *L. H. Pammel s. n.; W. D. Sterrett* 3; *S. M. Tracy* and *F. E. Lloyd* 4, 6, 7; Hinds Co., *H. Shearer s. n.;* Jackson Co., *D. Demaree* 33891, 33895, 34520; *E. Hilgard s. n.; C. H. Muller* 9766, 9767, 9768, 9769, 9770, 9772, 9958, 9965, 9967, 9969, 9970, 9976, 9977; *C. L. Pollard* 1208;

Figs. 1-6.—*Quercus virginiana, Q. fusiformis* and *Q. brandegei.* 1.—*Q. virginiana* Mill. from Baldwin Co., Alabama, *C. H. Muller 9779.* 2.—*Q. virginiana* Mill. from Wakulla Co., Florida, *R. K. Godfrey et al. 53921.* 3.—*Q. virginiana* Mill. (juvenile) from Georgetown Co., South Carolina, *C. H. Muller 3861.* 4.—*Q. fusiformis* Small from Brown Co., Texas, *C. H. Muller 8778.* 5.—*Q. fusiformis* Small from Nuevo Leon, Mexico, *J. E. Villareal 2160.* 6.—*Q. brandegei* Goldm. from Baja California (Cape Region), Mexico, *A. Carter et al. 2173.*

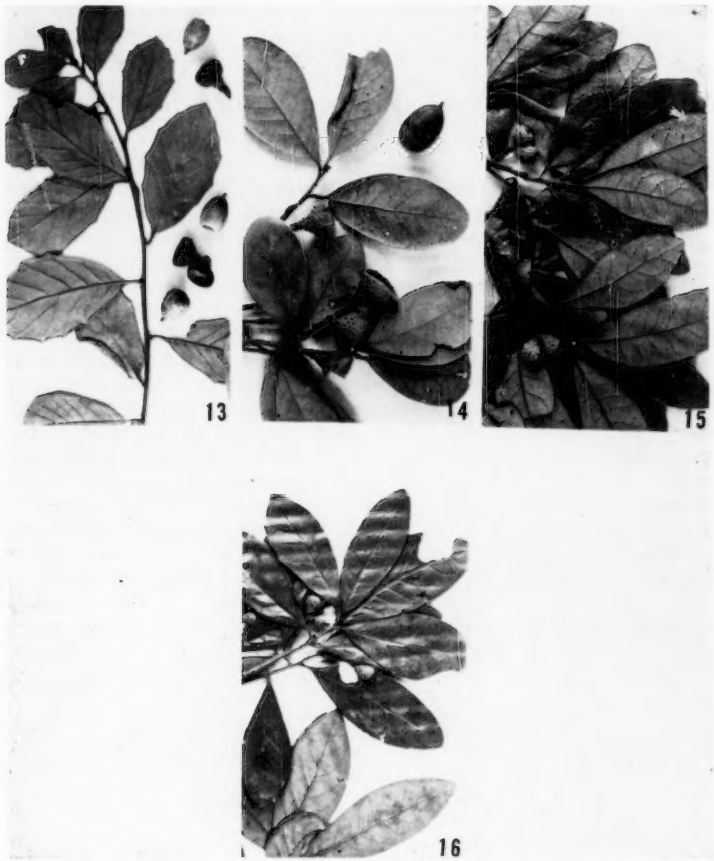
J. Skehan 22497; Jefferson Co., *W. B. McDougall* 1178, 1180; Wilkinson Co., *C. H. Muller* 10240.

LOUISIANA: Concordia Parish, *J. Donnell Smith s. n.;* Iberia Parish, *A. P. Beilmann s. n.; F. W. Russe Jr.* 6; Natchitoches Parish, *Engelmann s. n.; W. D. Sterrett* 36; Orleans Parish, *T. J. Burrill s. n.; Riddell s. n.;* St. Mary

Figs. 7-12.—*Quercus brandegei, Q. minima* and *Q. geminata.* 7.—*Q. brandegei* Goldm. from Baja California (Cape Region), Mexico, *F. Hester 6.* 8.—*Q. minima* Small from Franklin Co., Florida, *C. H. Muller 9802.* 9.—*Q.* minima Small from Clay Co., Florida, *C. H. Muller 10327.* 10.—*Q. minima* Small X *Q. Chapmani* Sarg. from Broward Co., Florida, *J. K. Small* and *J. J. Carter 1244* (type of *Q. rolfsii* Small). 11.—*Q. geminata* Small from Charleston Co., South Carolina, *K. W. Hunt 2823.* 12.—*Q. geminata* Small from Taylor Co., Florida, *C. H. Muller 9823.*

Parish, *W. D. Sterrett* 9, 11, 13; St. Tammany Parish, *Cocks* 4722; *G. Arsène* 11590, 11742, 12421, 12423, 12428, 12434, 12440, 12441, 12451, 12452, 12454, 12455, 12457, 12460, 12461, 12462, 12466, 12475, 12499, 12500, 12501, 12516; *C. H. Muller* 10256; Tangipahoa Parish, *Cocks* 4716 (type of *Q. virginiana var. eximea* Sarg.); Terre Bonne Parish, *C. H. Muller* 9762; Parish undetermined, *Carpenter s. n.; C. S. Sargent s. n.*

TEXAS: Aransas Co., *A. Chase* 6046, 4058; *H. von Schrenk* 3; Brazoria



Figs. 13-16.—*Quercus oleoides* and *Q. oleoides* var. *Sagraeana*. 13.—*Q. oleoides* Schl. & Cham. from Veracruz, Mexico, *C. H. Muller 9477*. 14.—*Q. oleoides* Sch. & Cham. from Honduras, *P. Shank 10782*. 15.—*Q. oleoides* var. *sagraeana* (Nutt.) C. H. Mull., from Prov. Pinar del Rio, Cuba, *C. H. Muller 9851*. 16.—*Q. oleoides* var. *sagraeana* (Nutt.) C. H. Mull., from Prov. Pinar del Rio. Cuba, *C. H. Muller 9877*.

Co., *B. F. Bush* 867; *C. H. Muller* 9759, 9760; *F. Lindheimer s. n.; E. J. Palmer* 5108; *W. D. Sterrett* 2, 7; *G. B. Sudworth s. n.;* Brooks Co., *C. H. Muller* 8047, 8048, 9683, 9684; Calhoun Co., *C. H. Muller* 3921, 5162, 10028, 10029, 10030, 10031, 10032, 10033, 10034, 10035, 10037, 10038, 10039, 10040, 10041, 10042, 10043, 10044, 10045, 10046, 10047, 10048, 10049, 10050, 10051, 10052, 10053, 10054, 10055a; *B. C. Tharp s. n.;* Chambers Co., *C. H. Muller* 10084; Harris Co., *A. Hayden* 18, 19; Jackson Co., *J. A. Drushel* 10179; *C. H. Muller* 3923, 5099; Jefferson Co., *C. H. Muller* 9761; Kenedy Co., *Bomhard 1; C. H. Muller* 5016, 5017, 9483; Kleberg Co., *E. R. Bogusch* S-89; Matagordo Co., *F. Lindheimer s. n.; E. J. Palmer* 9737; San Patricio Co., *C. H. Muller* 9753, 9754, 9757.

2. *Quercus fusiformis* Small, *Bull. Torr. Bot. Club* 28:357. 1901.
Q. virginiana var. *fusiformis* Sarg., *Bot. Gaz.* 65:448. 1918.
Q. virginiana var. *macrophylla* Sarg., *Bot. Gaz.* 65:447. 1918.

Large rhizomatous shrub or a large tree with rough black bark and spreading crown. Twigs 1.5 to 2.5 mm thick, densely fulvous-tomentulose, glabrescent the second year or persistently pubescent. Buds about 1.5 mm long, subglobose, glossy dark red, puberulent; stipules about 2.5 mm long, subulate, pubescent, usually quickly caducous. Leaves evergreen, hard and coriaceous, 2 to 7 cm long, 0.5 to 2 cm broad, oblong to elliptic or obovate, very polymorphic (one form elongate and acute, another broad and rounded, with all intermediates), apices very acute or rarely broadly rounded, bases cuneate or rounded, entire or irregularly 1- or several-toothed, margins somewhat revolute or nearly flat, upper surface glossy and glabrous or sparsely stellate-puberulent especially near the base of the midrib, lower surface uniformly dense stellate-tomentulose, the hairs appressed upon a variable layer of waxy puberulence; veins 8 to 10 on each side with occasional intermediates, irregularly branched and anastomosing, very inconspicuous above or slightly raised, scarcely prominent beneath; petioles 2 to 8 mm long, densely tomentulose. Staminate catkins 3.5 to 4.5 cm long, rather loosely flowered on a sparsely tomentose and glandular peduncle, the hairy anthers somewhat exserted from the moderately pubescent calyx. Pistillate catkins 1.5 to 5.5 cm long, 2- or 3-flowered distally or many-flowered along their lengths. Fruit solitary, paired, or in threes on a coarse peduncle 1.5 to 8 cm long; cups 7 to 10 mm high, 7 to 12 mm broad, goblet-shaped, somewhat constricted basally, the scales moderately thickened basally, densely white-tomentose, the apices dark red and puberulent; acorns 1.5 to 2 cm long, 1 to 1.3 cm broad, narrowly ovoid to subfusiform, glabrous and dull brown, one-third or one-half included.

Range.—Piedmont and coastal plain, from Oklahoma and the Edwards Plateau region of Texas south along the Sierra Madre Oriental and outlying ranges of Coahuila and Nuevo Leon into southern Tamaulipas.

The form of *Quercus fusiformis* with elongate and acute leaves with plain margins and very elongate fruiting peduncles which is concentrated in northeastern Mexico is reminiscent of *Q. brandegei.* The broad and obtuse leaves and shorter peduncles of the Edwards

Plateau and coastal plain populations of Texas more nearly approach *Q. virginiana* whose influence apparently differentiated this species from *Q. brandegei*. The Texan form of *Q. fusiformis* extends also into Mexico.

In previous treatments (e.g., Sargent, 1918; Trelease, 1924; Muller, 1951b) all of the coastal plain population was regarded as belonging to *Q. virginiana* while only the extremes of the thick-leafed shrubby form of the Edwards Plateau and adjacent Mexico were referred to *Q. fusiformis*. In the present treatment the entire Texan population is included in *Q. fusiformis* except for a small portion in the extreme southeast corner of Texas which gradually diminishes in prominence as it extends westward along the immediate coast. This modification has resulted from the application of a different method which might well be explained here.

Certain similarities of the Mexican portion of *Q. fusiformis* to *Q. brandegei* of Baja California early suggested the hypothesis that *Q. fusiformis* was differentiated from *Q. brandegei* under the influence of introgression *by Q. virginiana*. A biometric analysis of the three populations (in press elsewhere) confirmed this hypothesis. It became obvious that the best method of distinguishing between *Q. virginiana* and *Q. fusiformis* lay in the use of those characters in which *Q. virginiana* and *Q. brandegei* differ. This *a priori* choice of distinguishing characters could be valid, of course, only if the hypothesis of hybrid origin were correct. Their use, therefore, required the previous application of the biometric analysis. The three principal differences are fruit shape, leaf shape, and pubescence of the lower blade surface. In all three of these *Q. fusiformis* is intermediate between *Q. brandegei* and *Q. virginiana*. Since there exists also a high degree of correlation amongst them, it follows that these are better characters for the distinction of *Q. fusiformis* from *Q. virginiana* than the much less fundamental character of habit upon which *Q. fusiformis* was largely based.

The strict application of the criteria thus chosen has resulted in a separation between species that coincides with a geographic and ecological difference of great import. East of the Sabine River, *Q. virginiana* occurs on a variety of soils (except pure sand) along the immediate coast. Its occurrence inland in Louisiana, Florida, and Georgia appears to be dependent upon low elevation coincident with old beach lines. This extreme restriction to maritime situations continues into Texas in those specimens lacking characters of *Q. brandegei*. This latter species is widely distributed on piedmont slopes and along canyon floors in the Cape Region of Baja California. Although individuals of *Q. fusiformis* may closely approach the coast, no typical *Q. virginiana* extends very far inland from the coast. The inland forms carry some of the morphological characters of *Q. brandegei* and apparently also its ecological characters which permit them to grow in piedmont and other inland situations.

In the southwestern extremity of the range of *Q. virginiana,* its

distinction from *Q. fusiformis* is confused by what is apparently introgression of both by *Q. oleoides*. The liveoaks of the triangle bounded by Frio, Kenedy, and Calhoun Counties, Texas, clearly exhibit some characters of *Q. oleoides*. No acceptable solution of this problem is as yet possible. Graphic analysis of a three-fold introgression is notoriously difficult in any situation, but the fact that some of the characters of *Q. oleoides* obscure the best diagnostic characters of *Q. virginiana* makes this problem manifestly impossible.

In the light of this difficulty we are perhaps not justified in drawing any conclusions more definite than these: (1) there exists some correlation between the incidence of characters of *Q. oleoides* and the distribution of live oaks on dune sand areas along the Texas coast and on the coastal plain; (2) the obscurity of the distinction between *Q. virginiana* and *Q. fusiformis* in the same general area is due to the presence of *Q. oleoides* characters in the population; (3) some of the specimens (here cited under *Q. virginiana*) do not rightly pertain to that species *sensu strictu* and cannot be referred elsewhere with confidence.

It should be pointed out that *Q. oleoides* var. *quaterna* was described on the basis of this melange. Unfortunately, the type of this variety belongs to *Q. fusiformis* and the residual group is once more without a name. I propose to leave it unnamed within *Q. virginiana* with emphasis upon the fact that it owes its unique variability to the genetic influences of *Q. oleoides* and *Q. brandegei* (through *Q. fusiformis*).

Specimens examined:

OKLAHOMA: Comanche Co., *T. G. Harbison s. n.; C. H. Muller* 10161, 10162, 10163; *G. T. Robbins* 2859; Kiowa Co., *U. T. Waterfall* 11265.

TEXAS: Atascosa Co., *V. L. Cory* 11672; *E. J. Palmer* 10787, 10792, 11234, 12915; Austin Co., *H. Wurzlow s. n.;* Bastrop Co., *E. R. Bogusch* 1086; Bell Co., *S. E. Wolff* 3407; Bexar Co., *L. Berlandier* 984; *B. F. Bush* 1268; *H. Eggert s. n.; V. Havard s. n.; G. Jermy s. n.;* Blanco Co., *C. H. Muller* 8702; Bosque Co., *L. H. Shinners* 10419; Brown Co., *C. H. Muller* 8778; *E. J. Palmer* 26779, 29498; *H. L. Shantz s. n.;* Burnet Co., *Gould, Brown* and *Celerier* 5479; *collector undetermined* (Biltmore collection) 14888; Callahan Co., *C. H. Muller* 8790; Coke Co., *C. H. Muller* 8671; *E. J. Palmer* 12464; Coleman Co., *C. H. Muller* 8782; Colorado Co., *J. Byars s. n.;* Comal Co., *F. Lindheimer* 332, 520, 1184, 1185, 1186, 1187, 1188; *E. J. Palmer* 12202; Concho Co., *C. H. Muller* 8676; Crockett Co., *C. H. Muller* 5152; Dallas Co., *V. L. Cory* 243; De Witt Co., *V. L. Cory* 26582; *C. H. Muller* 3913; *M. Riedel s. n.;* Dimmit Co., *E. J. Palmer* 33777; Duval Co., *C. H. Muller* 8056; Eastland Co., *C. H. Muller* 8763; Edwards Co., *V. Bailey s. n.; F. Shreve* 9926; Erath Co., *L. C. Gough* s. n.; Frio Co., *C. H. Muller* 5019; *W. Trelease s. n.;* Galveston Co., *F. W. Mally s. n.;* Gillespie Co., *G. Jermy* 99, 100; Goliad Co., *M. Bomhard IV; H. Eggert s. n.; C. H. Muller* 8034; Grayson Co., *E. F. Owens* 509, 702; Hays Co., *E. J. Palmer* 12100, 12130; Hood Co., *H. Eggert s. n.; E. J. Palmer* 6508; *L. H. Shinners* 10348; Karnes Co., *Johnson* 1609; Kendall Co., *E. J. Palmer* 9816; Kerr Co., *V. L. Cory* 52387, 52388; *Lacey s. n.* (type); *E. J. Palmer* 12224; *A. A. Heller* 1616; Kimble Co., *D. Axelrod s. n.; C. H. Muller* 3952, 3952A; Kinney Co., *V. L. Cory* and *H. B. Parks* 26630; *E. A. Mearns* 1326, 1369, 1415; *C. H. Muller*

5043; Lampasas Co., *C. H. Muller* 8692; La Salle Co., *E. J. Palmer* 11292; Lavaca Co., *G. L. Fisher s. n.;* Lee Co., *E. Hall* 599; Llano Co., *G. L. Fisher* 37177; *B. C. Tharp s. n.;* Mason Co., *C. H. Muller* 8679; Maverick Co., *C. H. Muller* 4058; *Schott s. n.;* McLennan Co., *C. H. Muller* 3900; Menard Co., *L. C. Hinckley* and *L. Hinckley* 175; *C. H. Muller* 5026; *E. J. Palmer* 11896; Nolan Co., *C. H. Muller* 8670; *E. J. Palmer* 13749; Nueces Co., *A. A. Heller* 1542; Pecos Co., *M. E. Jones* 26069; *C. H. Muller* 5047; San Patricio Co., *A. A. Heller* 1569; San Saba Co., *E. J. Palmer* 11779, 11786, 11787, 11847; Shackelford Co., *C. H. Muller* 8563; Somervel Co., *L. F. Ward s. n.;* Stephens Co., *C. H. Muller* 8759; Sutton Co., *E. O. Wooton s. n.;* Tarrant Co., *G. W. Letterman s. n.; J. Reverchon* 910; *A. Ruth* 648; Taylor Co., *W. L. Tolstead* 5796; Terrell Co., *L. C. Hinckley* and *L. Hinckley* 377; *G. L. Webster* 491; Tom Green Co., *C. H. Muller* 8675; *E. J. Palmer* 12402; *M. Soulard s. n.; E. O. Wooton s. n.;* Travis Co., *E. Hall* 598; *W. H. Morgan* 3791; *C. H. Muller* 3942; *R. H. Painter* 141, 142, 143; *R. W. Strandtmann s. n.; B. C. Tharp* 8434, 44434; *M. S. Young s. n.;* Uvalde Co., *H. C. Cutler* 798; *I. M. Johnston* and *C. H. Muller* 1; *C. H. Muller* 5091, 5091A; *Edw. Palmer* 1279 (*pro parte,* cf. also *Q. virginiana*); *H. von Schrenck s. n.; E. Whitehouse* 603; Valverde Co., *H. C. Hanson* 443; *I. M. Johnston* and *C. H. Muller* 5, 6; *E. J. Palmer* 12954; *J. N. Rose* and *W. R. Fitch* 17960; Victoria Co., *J. D. Mitchell s. n.; C. H. Muller* 3918, 3919 (type of *Q. oleoides* var. *quaterna*), 3920; Washington Co., *E. Brackett s. n.;* Williamson Co., *C. H. Muller* 8718; *Edw. Palmer* 1280; Wilson Co., *E. J. Palmer* 9199; Young Co., *J. Reverchon s. n.;* County undetermined, *L. Berlandier* 266 and/or 543, 774 and/or 930, 2360, 2414, 2473, 2476; *J. M. Bigelow* 127, *s. n.; S. F. Blake* 1379; *B. E. Fernow s. n.; V. Havard s. n.; F. Lindheimer* 31790; *E. F. Owens* 510; *Edw. Palmer* 1276; *J. Reverchon* 3670; *C. Wright s. n.*

MEXICO: Coahuila, *E. Marsh* 518; *Edw. Palmer* 299, 1274; *F. L. Wynd* and *C. H. Muller* 285; Nuevo Leon, *L. Berlandier* 1335; *W. H. Canby, C. S. Sargent* and *W. Trelease* 227; *J. A. Drushel* 9695, 9696; *M. T. Edwards* 294; *Fernand* 2169; *A. Gavia* 2169; *J. Gregg* 222; *Grizzly s. n.; L. A. Kenoyer s. n.; Manning* and *Manning* 53400a; *M. Martinez* 21; *C. H. Muller* 580, 581, 2013, 2669; *C. G. Pringle* 2099; *C. S. Sargent s. n.; R. A. Schneider* 1122; *W. Trelease* 119; *J. E. Villarreal* 2156, 2160; *S. S. White* 1462; Tamaulipas, *H. H. Bartlett* 10001, 10766, 10901; *H. S. Gentry* 6747; *Manning* 53382; *M. Martinez* 53; *C. H. Muller* 9685, 9686, 9687, 9689; *Edw. Palmer* 264; *A. J. Sharp, H. A. Crum* and *W. B. Fox* 50323; *H. W. Viereck* 301.

3. *Quercus brandegei* Goldm., *Contr. U. S. Nat. Herb.* 16:321. 1916.

Moderate or large tree to 18 m tall with furrowed gray bark and broad spreading crown. Twigs 1.5 to 2.5 mm in diameter, densely stellate-tomentulose and waxy puberulent, at length glabrate or variously persistently pubescent. Buds about 1.5 mm long, subglobose, glossy dark red, puberulent; stipules about 3 mm long, subulate, pubescent, usually deciduous. Leaves evergreen, hard and coriaceous, 3 to 7 cm long, 1 to 2 or rarely 3 cm broad, elongate-oblong or sometimes narrowly elliptic, acute or rarely obtuse, basally rounded or merely obtuse, entire or irregularly coarsely 1- to several-toothed, the margins flat or very slightly revolute, upper surface glabrous and glossy or sparsely stellate-puberulent especially about the base of the midrib, lower surface uniformly canescent-stellate-tomentulose, the

hairs appressed upon a dense waxy puberulence; veins about 8 or 10 on each side with irregular intermediates, variously branching and anastomosing, inconspicuously raised on both surfaces; petioles 2 to 7 mm long, densely tomentulose. Staminate catkins about 2.5 to 3.5 cm long, moderately loosely flowered on a densely tomentulose peduncle, the pubescent anthers moderately exserted from the pubescent calyx. Pistillate catkins 1 to 3 or more cm long, 1- to 3-flowered at the apex. Fruit solitary or paired on a coarse peduncle to 6 cm long; cups about 12 mm high and 12 mm broad, deeply goblet-shaped, usually markedly constricted basally, the scales basally thickened and densely white-tomentose, the apices dark red and puberulent; acorns 3 to 4.5 cm long, 1 to 1.2 cm broad, fusiform, the apex attenuately beaked, glabrous and dull brown with a glaucous bloom, one-fourth or less included.

Range.—Piedmont of the Sierra de la Laguna, Cape Region of Baja California, Mexico.

Quercus brandegei is unique in the series *Virentes* in the extremely fusiform acorns and its great isolation from the other members of the series. Furthermore, it occupies generally more rocky and well-drained sites than the other members of the group, a character it shares with *Q. fusiformis*, its closest relative.

Specimens examined:

MEXICO: Baja California, *T. S. Brandegee s. n.; A. Carter* 2713; *A. Carter, A. M. Alexander* and *L. Kellogg* 2173, 2455; *H. S. Gentry* 4361, 11830; *H. S. Gentry* and *W. B. Fox* 11866; *F. Hester* 2, 3, 4, 5, 6, 7, 8; *M. E. Jones* 24476, 24477; *M. Martinez* 6; *C. H. Muller* 10548, 10549, 10550, 10551, 10597, 10598, 10599; *E. W. Nelson* and *E. A. Goldman* 7422, 7475 (type); *I. L. Wiggins* 5640.

4. *Quercus minima* Small, *Bull. Torr. Bot. Club* 24:438. 1897.

Q. virens var. *dentata* Chapm. *Fl. So. St.* 421. 1860.
Q. virginiana var. *minima* Sarg. *Silva* 8:101. 1895.
Q. succulenta Small, *Fl. S.E.U.S.* 2 ed. 1332. 1913.
Q. virginiana var. *dentata* Sarg., *Bot. Gaz.* 65:448. 1918.
Q. geminata var. *succulenta* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.

Shrub 2 to 10 dm tall spreading by rhizomes. Twigs 1.5 to 2 mm thick, from densely silvery or fulvous stellate-tomentulose at length glabrate and dark red. Buds about 1.5 mm long, subglobose, glossy red, sparingly pubescent; stipules about 3 mm long, subulate, sparingly pubescent, quickly caducous. Leaves evergreen, hard and coriaceous, highly (constantly) polymorphic, the individual plants rarely uniform for one leaf type, the lower leaves characteristically large and toothed or lobed, the upper usually narrowly oblong and entire, the narrow upper leaves tending to hold their pubescence more persistently than the broad lower ones, the narrow form 2 to 5.5 cm long, 0.5 to 1.6 cm broad, oblanceolate, entire or few-toothed near the acute or rounded apex, the base narrowly cuneate, the broad form 4.5 to 11.5 cm long, 2 to 5 cm broad, broadly oblanceolate to narrowly obovate, coarsely

and irregularly toothed in the upper half or full length, obtuse or acute, broadly cuneate, margins slightly revolute, upper surface glabrous and glossy or sparingly stellate about the base of the midrib, lower surface densely or sparsely silvery appressed-stellate-puberulent, this persistent or on some of the broad lower leaves variously deciduous, the midrib and principal veins glabrous; veins 4 to 12 on each side, very irregular, the higher numbers in the narrow leaves, much branched and obviously anastomosing, slightly raised above, rather prominent beneath, the reticulum obscure; petioles 1 to 5 mm long, stellate-pubescent. Staminate catkins 4 to 5 cm long, rather loosely flowered, the peduncle fulvous-stellate-tomentulose, the pubescent anthers finally well exserted from the pubescent calyx. Pistillate catkins 3 to 10 cm long, 2-to several-flowered, the peduncle fulvous-pubescent but glabrate with the twigs. Fruit solitary or paired on peduncles 0.5 to 3 cm long; cup 8 to 16 mm high, 10 to 15 mm broad (in one form only 5 mm high and 7 mm broad), deeply goblet-shaped, usually markedly constricted basally, the scales silvery tomentose with puberulent or glabrous red apices protruding, the bases sometimes strongly thickened; acorns 15 to 20 mm long, 8 to 12 mm broad (in one form smaller), glabrous and rather glossy brown, one-fourth to one-third included or more.

Range.—Sandy coastal plain, southeastern North Carolina, Georgia, Florida, and Mississippi.

While no type specimen was designated for *Quercus virens* var. *dentata*, there exists in the herbarium of the New York Botanic Garden a mixture of material collected by Chapman about Apalachicola some of which represents the present concept of *Q. minima*. The species is typified by Sargent's plate 396 (Silva 8:101. 1895), while the element of this mixture illustrated by Trelease (Mem. Nat. Acad. Sci. 20: pl. 201A. 1924) is a hybrid of *Q. minima* and *Q. geminata*. These two species frequently occur together, the latter usually on the deeper sand substrata, and sporadic hybrids between them are occasionally encountered. The aberrant form designated as *Q. succulenta* Small (and *Q. geminata* var. *succulenta* Trel.) owes its resemblance to *Q. geminata* to this origin.

Although *Quercus minima* overlaps the range of *Q. virginiana*, its restriction to sand substrata apparently so isolates it from the clay-inhabiting tree species that no great hybridization occurs and the two remain distinct. The free fruiting of *Q. minima* in the form of a low rhizomatous shrub readily distinguishes it from the rhizomatous juvenile form of *Q. virginiana* (in which the twig pubescence and leaf characters are also distinctive).

Specimens examined:

NORTH CAROLINA: Brunswick Co., *W. W. Ashe s. n.*

SOUTH CAROLINA: Beaufort Co., *A. Cuthbert* 718; *J. H. Mellichamp s. n.*

GEORGIA: Camden Co., *F. S. Blanton* 6450; Charlton Co., *W. W. Ashe s. n.; W. H. Duncan* 7434; McIntosh Co., *C. H. Muller* 9926, 9927, 9930; Mitchell Co., *R. M. Harper* 1167; County undetermined, *R. M. Harper* 1577.

FLORIDA: Alachua Co., *W. W. Ashe s. n.; T. G. Harbison* 5306; Baker

Co., *W. W. Ashe s. n.*; Bay Co., *W. W. Ashe s. n.*; *H. J. Banker* 3495; Brevard Co., *A. Fredholm* 5739, 5768, 5779, 6064; *G. G. Hedgcock s. n.*; Calhoun Co., *C. H. Muller* 10480, 10481; Clay Co., *C. H. Muller* 10326, 10327; Dade Co., *H. C. Cowles s. n.*; *H. N. Moldenke* 717, 777, 3666, 5461, 5667; *C. A. Mosier s. n.*; *F. Rugel s. n.*; *W. E. Safford s. n.*; *C. L. Simpson s. n.*; *J. K. Small* 7266, *s. n.*; *J. K. Small* and *J. J. Carter* 550, 2481; *G. B. Sudworth s. n.*; Dixie Co., *C. H. Muller* 10287; Duval Co., *A. H. Curtiss* 2591, 2597 and/or 4597 (*pro parte*, cf. also *Q. geminata*), 4190, 6432, 6432a, *s. n.*; *H. D. Keeler s. n.* (*pro parte*, cf. also *Q. virginiana*); Flagler Co., *C. H. Muller* 9900, 9901, 9913; Franklin Co., *A. W. Chapman s. n.* (type of *Q. virens* var. *dentata*); *C. H. Muller* 9802, 10258, 10259, 10269; *C. Mohr s. n.*; Highlands Co., *T. G. Harbison* 4617; *J. K. Small, J. P. DeWinkeler* and *C. A. Mosier* 11361; Lafayette Co., *T. G. Harbison* 5574; Lake Co., *G. V. Nash* 520, 1762; Lee Co., *J. N. Harshberger s. n.*; *A. S. Hitchcock* 338; *H. N. Moldenke* 1012; *J. P. Standley* 165, 289; Manatee Co., *C. H. Muller* 10295, 10296; *Reasoner Bros.* 405; *J. H. Simpson* 22; Okeechobee Co., *A. H. Howell* 1042; Osceola Co., *A. H. Howell* 993; *E. A. Mearns s. n.*; Putnam Co., *C. H. Muller* 10307, 10308, 10309, 10314, 10315; Seminole Co., *S. Rapp* 21; St. Johns Co., *J. A. Harris* 19896; Wakulla Co., *W. W. Ashe s. n.*; *C. H. Muller* 9816; Walton Co., C. H. Muller 9790, 9797; County undetermined, *A. W. Chapman s. n.*; *A. H. Curtiss s. n.*; *H. C. Cowles* 236, 237; *Hubbard s. n.*; *Leavenworth s. n.*; *J. K. Small s. n.*

MISSISSIPPI: Jackson Co., *C. H. Muller* 9963, 9964.

4a. *Quercus minima* Small × *Q. chapmani* Sarg.

Q. rolfsii Small, *Fl. S.E.U.S.*, 2 ed. 1332. 1913.
Q. geminata var. *succulenta* f. *rolfsii* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.

Low rhizomatous shrub. Twigs 1 to 2 mm thick, from densely fulvous-glandular or gray tomentulose soon glabrate and dark reddish brown. Buds about 1.5 or 2 mm long, subglobose, glabrous and glossy red. Stipules about 3 mm long, subulate, pubescent, soon caducous. Leaves evergreen, thin and coriaceous, 2.5 to 5 cm long, 1 to 2.5 cm broad, elliptic to oblong or narrowly obovate, broadly rounded apically and basally, coarsely or obscurely round-toothed or shallowly lobed about the apex or rarely entire, margins somewhat revolute, upper surface glossy and glabrous, lower surface dull, minutely and sparsely puberulent with appressed stellate and simple hairs; veins about 6 or 7 on each side with occasional intermediates, irregularly branching and obviously anastomosing, raised above and quite prominent beneath; petioles 1.5 to 2 mm long. Staminate catkins 3 to 4 cm long, rather loosely flowered on a densely stellate-pubescent peduncle, the pubescent anthers somewhat exserted from the slightly pubescent calyx. Pistillate catkins not seen. Fruit solitary or paired on a coarse peduncle 1 or 2 cm long; cup 12 to 15 mm high, about 14 mm broad, deeply goblet-shaped, strongly constricted basally, the scales basally thickened, silvery tomentose, the puberulent apices dark red; acorn 2 to 2.5 cm long, 0.9 to 1.2 cm broad, oblong, glabrous and glossy brown, about one-third to one-half included.

Range.—Coastal plain, local the full length of eastern Florida.

The tomentulose young twigs, pubescent anthers, and the fruit of this form are all typical of *Quercus minima* and its close relatives in the series *Virentes*, while the prompt glabrescence of the twigs, the leaf outline, and the sparse puberulence of the lower leaf surface are typical of *Q. chapmani*. These two species occur intermixed over many hundreds of square miles. The herbarium specimens identified as *Q. rolfsii* are few in number, but they represent widely separated portions of peninsular Florida. They exhibit some characters, notably size and shape of the fruit, which are not to be found in either *Q. minima* or *Q. chapmani*. The dismissal of *Q. rolfsii* as a hybrid of these two species was therefore impossible on the basis of existing herbarium material. A field study of the problem yielded populations of hybrids locally within the widespread association of the parents. In these typically back-crossing and segregating hybrid populations one invariably found some individuals with the characters of *Q. rolfsii* (e.g., *C. H. Muller 10323, 10324, 10325*). Those characteristics unique to this form apparently emerge from the complementary effect of *Q. minima* and *Q. chapmani* and are to be found only in the F_1 progeny (or similar intermediates) and not in those hybrids perceptibly diluted by either back-crossing or segregation.

The forms represented by *Quercus virginiana* var. *pygmaea* Sarg. (*Bot. Gaz.* 65:449. 1918.—*Q. minima* f. *pygmaea* Trel., *Mem. Nat. Acad. Sci.* 20:115. pl. 201B. 1924) and by *Q. minima* f. *reasoneri* Trel. (*l.c.*, pl. 200B, but "Quercus geminata reasoneri" on the plate) belong with *Q. chapmani*. If these are at all related genetically to the species of *Virentes*, it is through dilute hybridization.

Quercus chapmani Sarg., which Small regarded as a species of the series *Virentes*, appears rather to belong with *Q. sinuata* Walt. in the series *Durandieae* Trel. in which its appressed stellate pubescence of the lower leaf surface is typical, being extremely minute, silvery, and unmixed with trichomes of any other sort.

Specimens examined:

FLORIDA: Broward Co., *J. K. Small* and *J. J. Carter* 1244 (type of *Q. rolfsii* Small); *J. K. Small* and *P. Wilson s. n.*; Clay Co., *C. H. Muller* 10323, 10324, 10325; Orange Co., *Baker s. n.*

5. *Quercus geminata* Small, *Bull. Torr. Bot. Club* 24:438. 1897.

Q. virens var. *maritima* Chapm., *Fl. So. St.* 421. 1860. — not *Q. maritima* Willd., *Sp. Pl.* 4 ed. 4:424. 1805.
Q. virginiana var. *maritima* Sarg., *Silva* 8:100. 1895.
Q. virginiana var. *geminata* Sarg., *Bot. Gaz.* 65:445. 1918.
Q. virginiana var. *geminata* f. *grandifolia* Sarg., *Bot. Gaz.* 65:446. 1918.
Q. geminata f. *maritima* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.
Q. geminata var. *grandifolia* Trel., *Mem. Nat. Acad. Sci.* 20:115. 1924.

Small or moderate trees 2 to 12 m tall (or sometimes reaching 20 m) with rough hard furrowed bark. Twigs 2 to 3 mm thick, from fulvous and glandular velvety-stellate-tomentulose gradually glabrate, the lenticels scarcely prominent. Buds to 2.5 mm long, subglobose, red-

dish brown and sparingly puberulent; the stipules 3 to 4 mm long, concave-spatulate, sparsely pubescent, soon deciduous. Leaves evergreen or subevergreen, 3 to 6 or even 12 cm long, 1 to 3 or 4.5 cm broad, oblanceolate to obovate, acute or broadly rounded, basally tapered or rarely rounded, strictly entire, the margins strongly revolute and cartilaginous, the blade thick and leathery, nearly flat or characteristically strongly concave beneath, upper surface glossy and glabrous or a few stellate hairs persisting along the midrib near the base, lower surface (midrib and some veins excepted) densely and permanently fulvous or gray pubescent with a mixture of simple or branched puberulence and spreading stellate hairs; veins about 10 on each side with occasional intermediates, much branched and obviously anastomosing, markedly impressed above, very prominent (including the reticulum) beneath; petioles 3 to 10 mm long, stellately fulvous-glandular-pubescent. Staminate catkins about 4 to 6 cm long, rather loosely flowered, the peduncles glandular-pubescent, the hairy anthers at length exserted from the sparsely pubescent and ciliate calyces. Pistillate catkins 1 to 10 cm long, 2- or many-flowered along the fulvous-tomentulose peduncle. Fruit usually geminate or rarely solitary or more numerous; cups 10 to 13 or 15 mm broad, 8 to 10 mm high, basally constricted, margins simple, scales imbedded in dense lanate tomentum, the elongate apices merely puberulent and dark red; acorns 15 to 20 mm long, 9 to 12 mm broad, narrowly ovoid to subfusiform, obtuse or acute, glabrous and dull brown, about one-third included.

Range.—Coastal plain, especially along the immediate coast, on sandy soil or pure deep sand, North Carolina to Florida and westward to Mississippi and possibly Louisiana.

Since both *Quercus geminata* and *Q. minima* occur on sand in Florida, it is to be expected that two so closely related species would hybridize freely. Specimens of marked intermediate character are indeed to be found, these often having the pubescence and veins of *Q. geminata* and the low stature and tendency toward leaf toothing of *Q. minima*. The relative scarcity of such intermediates would indicate that an effective barrier to free crossing exists. Specific cases of such hybridization are discussed under *Q. minima*.

Willdenow's description of *Quercus maritima* clearly excludes what is here known as *Q. geminata* by its reference to leaves glabrous on both surfaces. The original misidentification seems to date back to Chapman whose *Q. virens* var. *maritima* is described as having leaves concave. Since t . .a Sargent and Trelease have applied the name *maritima* to forms of *Q. geminata*. Willdenow's *Q. maritima* is a member of the subgenus *Erythrobalanus*. It was based upon *Q. phellos β maritima* Michx. which was illustrated in the *Hist. Chenes Amer. Sept.* pl. 13, fig. 3, where the apical seta is clearly delineated. The type in the Michaux Herbarium at Paris is labelled *Q. phellos β viridis*. Authentic duplicates occur in the Willdenow Herbarium at Dahlem and at Kew. The Kew collection is a series of fragments of the types pre-

pared and annotated by Andres Michaux. Willdenow's herbarium contains in addition two specimens under *Q. maritima*, one of *Q. virginiana* and the other of *Q. hemispherica* Bartram (which his description fits). Since the type of *Q. phellos* β *maritima* is a form of *Q. hemispherica* still common on the Atlantic Coast of South Carolina (e.g., *C. H. Muller 10459, 10460, 10461*), this plant is **Q. hemispherica** var. **maritima** (Michx.) comb. nov.[2]

Specimens examined:

NORTH CAROLINA: Brunswick Co., *W. W. Ashe s. n.; E. J. Palmer* 39829; *collector undetermined* (Biltmore Herb.) 4450; New Hanover Co., *R. K. Godfrey* 4725; *T. F. Woods s. n., collector undetermined*, (Biltmore Herb.) 4453; county undetermined, *J. A. Harris* 19378.

SOUTH CAROLINA: Beaufort Co., *J. R. Churchill* 341; *J. H. Mellichamp s. n.; C. H. Muller* 9937, 9938; *C. S. Sargent s. n.;* Charlestown Co., *K. W. Hunt* 2823; *J. K. Small* and *L. M. Bragg s. n.*

GEORGIA: Coffee Co., *R. M. Harper* 2050; Glynn Co., *T. G. Harbison* 1325, 1331; *C. H. Muller* 9923, 9924, 9925; Irwin Co., *F. J. Hermann* 10062; McIntosh Co., *C. H. Muller* 9929; County undetermined, *T. G. Harbison s. n.*

FLORIDA: Alachua Co., *T. G. Harbison* 5351; Bay Co., *C. H. Muller* 9800; Brevard Co., *F. S. Blanton* 6301; *A. Fredholm* 5746; *C. H. Muller* 9887, 9888, 9891, 9892; Citrus Co., *O. Degner* 5175; Collier Co., *C. H. Muller* 9834; Colubia Co., *L. McCulloch s. n.; P. H. Rolfs s. n.;* De Soto Co., *C. H. Muller* 9832; Dixie Co., *C. H. Muller* 9825, 9826; Duval Co., *J. R. Churchill s. n.; A. H. Curtiss* 2597 and/or 4597 (*pro parte*, cf. also *Q. minima*), 4189, 4598, 5786; Flagler Co., *C. H. Muller* 9907, 9908; Franklin Co., *A. W. Chapman s. n.; Drummond* 31; *R. K. Godfrey* 54092; *C. H. Muller* 9805, 9806, 9807, 10260, 10270, 10275, 10276; Hernando Co., *C. H. Muller* 10294; Hillsborough Co., *A. P. Garber s. n.;* Highlands Co., *W. W. Ashe s. n.; T. G. Harbison* 4623, 4652, 4653; *J. K. Small* and *J. P. De Winkeler* 9039; Lafayette Co., *T. G. Harbison* 55, 4813; *E. J. Palmer* 27319; Lake Co., *G. V. Nash* 516, 1623, 2414 (type); Lee Co., *A. S. Hitchcock* 337; *H. N. Moldenke* 979, 1013; Leon Co., *Reese* 610; *A. Steward s. n.;* Levy Co., *C. D. Mell s. n.; Edw. Palmer* 7620; Liberty Co., *L. Hubricht* B2063; Manatee Co., *C. H. M. Barrett s. n.; J. H. Simpson* 57; Marion Co., *C. D. Mell s. n.; C. H. Muller* 9827, 9831; Martin Co., *C. H. Muller* 9883; *J. K. Small, J. W. Small* and *J. P. De Winkeler* 10707; Okaloosa Co., *C. H. Muller* 9781; *Wakely s. n.;* Okeechobee Co., *J. K. Small, N. L. Britton, E. G. Britton* and *J. P. De Winkeler* 9251C; Orange Co., *T. G. Harbison* 3783; Pasco Co., *H. O'Neill s. n.;* Pinellas Co., *F. Beckwith* 609; Polk Co., *W. W. Ashe s. n.; J. Donnell Smith s. n.; T. G. Harbison* 3; *C. H. Muller* 10297; Putnam Co., *C. H. Muller* 10310, 10465, 10470, 10472; Seminole Co., *S. Rapp* 7, 12, 13, *s. n.;* St. Johns Co., *A. H. Curtiss* 6427; *C. H. Muller* 9920; *A. Ruth s. n.; G. B. Sudworth s. n.; C. S. Williamson s. n.;* St. Lucie Co., *J. A. Harris* 21127; *A. H. Howell* 1026; *C H. Muller* 9884; *J. K. Small* and *J. P. De Winkeler* 9489; Taylor Co., *C. H. Muller* 9822, 9823; Volusia Co., *C. H. Muller* 9896; Wakulla Co., *C. H. Muller* 9810; Walton Co., *C. H. Muller* 9783, 9787, 9788, 9789, 9791, 9795, 9796; County undertermined, *A. W. Chapman s. n.; A. H. Curtiss s. n.; J. A. Harris* 21221; *F. Rugel* 98, 342, *s. n.; J. Schneck* 422, 424; *B. C. Tharp* 5404.

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[2] *Quercus phellos* β *maritima* Michx., *Hist. Chenes Amer. Sept.* pl. 13, fig. 3. 1801.

ALABAMA: Baldwin Co., *D. Demaree* 35890, 35896, 35935, 35959, 35960, 35965; Mobile Co., *C. Mohr, s. n.*

MISSISSIPPI: Harrison Co., *D. Demaree* 33674, 33675, 35087, 35814, 35818; *T. G. Harbison* 3656, 3659; *C. H. Muller* 9764, 9765, 9983, 9984, 9985, 9986, 9987, 10000, 10001, 10002, 10005, 10006; *C. L. Pollard* 1054; *W. D. Sterrett* 1, 4, 5; *S. M. Tracy* and *F. E. Lloyd* 2, 3; *S. M. Tracy* 5138, *s. n.*; Jackson Co., *D. Demaree* 33568, 33892, 33899, 33970, 34093, 34105, 34519; *C. Mohr s. n.*; *C. H. Muller* 9957, 9959, 9960, 9961, 9962, 9971, 9972, 9979, 9981, 9982.

LOUISIANA: St. Martin Parish, *A. B. Langlois* 13.

6. *Quercus oleoides* Schl. and Cham., *Linnaea* 5:79. 1830.
Q. lutescens Mart. & Gal., *Acad. Brux. Bul.* 10:219. 1843.
Q. retusa Liebm., *Overs. Danske Vidensk. Selsk. Forhandl.* 1854:187. 1854.
Q. tropicae Berl., *Soc. Mex. Geogr. y Estad. Bol.* 5:128. 1857 (nom. nud.).
Q. oleoides var. *australis* Trel., *Mem. Nat. Acad. Sci.* 20:114. 1924.
Q. oleoides f. *lutescens* Trel., *Mem. Nat. Acad. Sci.* 20:114. 1924.

Small or large tree with spreading crown and rough hard dark bark. Twigs 1 to usually 2 to 3 mm in diameter, moderately or densely fulvous-glandular, puberulent or tomentulose with a mixture of simple and stellate hairs, at length glabrate or persistently pubescent. Buds about 2 to 3 mm long, subglobose or angular, glabrous and glossy dark red or gray-puberulent; stipules subulate, pubescent, quickly caducous. Leaves evergreen, rather thick and coriaceous, 4 to 10 or even 14 cm long, 2.5 to 5 or 7.5 cm broad, apically obtuse or sometimes acute or rounded or even retuse, basally cuneate, obovate to oblong or broadly oblanceolate, entire or exceptionally coarsely toothed especially above the middle, upper surface glossy and glabrous except the densely stellate-tomentulose midrib near the base, lower surface (except for the midrib and principal veins) densely fulvous or silvery appressed-stellate-tomentulose and frequently with spreading stellate hairs in addition; veins about 5 to 7 on each side and with occasional intermediates, strongly branched and obviously anastomosing, inconspicuous above or sometimes impressed, rather prominent beneath, often including the reticulum; petioles 4 to 10 or 12 mm long, densely fulvous-puberulent. Staminate catkins about 4.5 to 5.5 cm long, the peduncle fulvous-pubescent and moderately densely flowered, the markedly pubescent anthers well exserted from the very sparsely pubescent calyx. Pistillate catkins 1 to 6 cm long, 1- to several-flowered, the peduncle fulvous-glandular-tomentulose. Fruit solitary or paired; cup 12 to 15 or rarely 20 mm broad, 8 to 12 or rarely 20 mm high, deeply goblet-shaped, basally constricted, the scales sometimes markedly thickened basally, occasionally markedly vertically seriate, rather uniformly gray or silvery or tan pubescent throughout or the rather short apices less markedly so; acorn 20 to 25 mm long, 9 to 13 or rarely 16 mm broad, glabrous and rather dull brown, one-third or nearly one-half included.

Range.—Coastal plain and Piedmont, central Tamaulipas to Costa Rica, apparently confined to the Atlantic slope.

Quercus oleoides has a fairly wide tolerance of soil types. Although it is found on gravelly clay soils over much of its range, in coastal

Tamaulipas and adjacent Veracruz it occurs extensively on both clays and deep sands. The young plants are clearly rhizomatous and form small clumps prior to the assumption of tree form. The presence of spreading stellate hairs on the lower leaf surface and the occasional impression of the veins on the upper surface are characters of *Q. geminata* derived through the Cuban *Q. oleoides* var. *sagraeana*. These are encountered in *Q. oleoides* principally in the Veracruz population and scarcely appear below the Yucatan Peninsula. Conversely, the vertically seriate cup scales characteristic of a portion of the Veracruz population are observed occasionally in the Cuban variety and less frequently elsewhere.

Specimens examined:

MEXICO: Chiapas, *J. Bermudez* 2255, 2257, 2261, 2266; *M. Martinez* 374, 375, 387; *E. Matuda* 3732; *F. Miranda* 7201; Hidalgo, *H. E. Moore, Jr.* 3010; Oaxaca, *C. Conzatti* 3845; *L. S. Hernandez* 2260; *T. MacDougall* 2445, 2533, 2550; *M. Martinez* 690; *C. D. Mell* 27; *C. H. Muller* 9743, 9744, 9748; Puebla, *H. Bravo* 2068, 2069, 2379; *C. H. Muller* 9722, 9723, 9724, 9725, 9726, 9727; San Luis Potosi, *M. T. Edwards* 562; *C. H. Muller* 9701, 9702; *L. M. Palafox* 2133; *J. Rzedowski* 6996; Tabasco, *E. Matuda* 3129; *J. A. Peralta* 2113; Tamaulipas, *L. Berlandier* 2194 (= 774) (type of *Q. tropicae*); *P. S. Martin* 047, 049, 114, 115; *C. H. Muller* 9479, 9480, 9481, 9482, 9691, 9692, 9693B, 9694, 9696, 9697, 9698, 9699, 9700; *Edw. Palmer* 220, 318; Vera Cruz, *E. A. Goldman* 727; *H. Le Sueur* 86; *F. Liebmann* 3528; *J. J. Linden* 26; *E. Matuda* 1453; *C. D. Mell s. n.; F. Miranda* 7108; *D. Mojica* 2176; *C. H. Muller* 9477, 9478, 9728, 9729, 9730, 9730A, 9733, 9734, 9735, 9736, 9737, 9738, 9740, 9742; *E. W. Nelson* 67, 80; *C. A. Purpus* 6166, *s. n.; C. J. W. Schiede* 14 (Cotype), *R. Vorrath* 2277, 2278, 2279; Yucatan, *T. J. Burrill* 26513; State undetermined, *L. Berlandier* 543 (*pro parte*, cf. also *Q. fusiformis*); *F. Liebmann s. n.; C. A. Purpus* 14245.

GUATEMALA: *H. H. Bartlett* 12112; *S. F. Blake* 7735; *O. F. Cook* and *R. F. Griggs* 318; *C. C. Deam* 159; *Friedrichsthal s. n.; C. Galusser* 1; *H. Pittier* 1789, 1818.

BRITISH HONDURAS: *H. H. Bartlett* 11203, 11204, 11308, 11313, 11552, 11553, 11873, 11886, 12976, 12979; *P. H. Gentle* 2695, 3378, 3792, 4072, 4156, 4162; *C. L. Lundell* 4347, 6627, 6837, 6964; *Kinloch* 97; *H. O'Neill* 8554, 8555; *W. A. Schipp* 209, 672.

HONDURAS: *P. H. Allen* 3887; *J. B. Edwards* 323, 375, 578; *A. Molina R.* 5, 7, 16, 492; *S. J. Record* and *H. Kuylen* 53, 53A; *P. Shank* 10782; *P. C. Standley* 861, 1356, 1366; *P. C. Standley* and *P. Chacon* 5684; *P. C. Standley* and *H. O. Lindelie* 7302; *C. Thieme* 5615; *W. von Hagen* and *C. von Hagen* 1095; *H. N. Whitford* and *L. R. Stadtmiller* 41, 55; *L. O. Williams* and *A. Molina R.* 10046, 10054, 11030, 12259; *T. G. Yuncker, J. M. Koepper* and *K. A. Wagner* 8179.

COSTA RICA: *A. M. Brenes* 15590; *C. W. Dodge* and *W. S. Thomas* 6232; *H. Pittier* 2127, 2607 (isotype of *Q. oleoides* var. *australis*).

6a. **Quercus oleoides** var. **sagraeana** (Nutt.) C. H. Mull., comb. nov.

Q. sagraeana Nutt., *Sylva* 1:17. 1842.

Q. cubana Richard, *Fl. Cuba* 3:230. 1853.

Q. virginiana var. *sagraeana* Trel., *Mem. Nat. Acad. Sci.* 20:113. 1924.

Small or large trees with spreading crowns and rough gray or dark bark. Twigs 1.5 to 2.5 mm in diameter, persistently fulvous-glandular-

tomentulose or at length glabrate. Buds about 2 mm long, subglobose or obscurely round-angled, dark red, sparsely puberulent; stipules subulate, pubescent, quickly caducous. Leaves evergreen, hard and coriaceous, 3 to 9 cm long, 1 to 3.5 cm broad, oblong to obovate or broadly oblanceolate, acute to obtuse or even broadly rounded, entire or frequently coarsely and irregularly toothed, the margins strongly revolute, the blade nearly flat or markedly concave, upper surface glabrous and glossy except the persistently stellate-pubescent midrib and principal veins, lower surface characteristically minutely dense-tomentulose with a mixture of simple and stellate appressed hairs, fulvous-glandular or silvery, but commonly also with spreading stellate tawny hairs, the midrib and principal veins nearly glabrous; veins 8 or 9 on each side, strongly branched and obviously anastomosing, rather markedly impressed above, very prominent (including the reticulum) beneath; petioles 2 to 10 mm long, densely fulvous-tomentulose. Staminate catkins about 5 cm long, rather loosely flowered, the pubescent anthers little exserted. Pistillate catkins 1 to 3 or 4 cm long, 2- or 3-flowered on a fulvous-tomentulose peduncle. Fruit solitary or paired, the coarse peduncle fulvous-tomentulose; cup 12 to 20 mm broad, 10 to 20 mm high, deeply cup-shaped, basally usually markedly constricted, the scales basally thickened and densely fulvous-tomentose, the dark red apices thin and puberulent; acorn about 20 to 25 mm long, 12 to 15 mm broad, ovoid, glabrous and dull or glossy brown, about one-third included.

Range.—Coastal plain and uplands of the Pinar del Rio province, Cuba.

The forms of *Quercus oleoides* var. *sagraeana* with plane leaves, less prominent veins, and lacking the loosely spreading stellate hairs on the lower surface are usually characterized by fruits in which the cup scales are strongly seriate as in much of *Q. oleoides*. Those foliage specimens most suggestive of *Q. geminata*, on the other hand, are associated with cups the scales of which are not markedly seriate and which might readily be accepted within *Q. geminata*. The population, although somewhat variable, is rather well distinguished from *Q. oleoides* by shape, concavity, venation, and pubescence of the leaves and from *Q. geminata* by the mitigation of these characters with the flat blades, short pubescence, and inconspicuous veins of *Q. oleoides*. The origin of the variety as a hybrid swarm of *Q. oleoides* and *Q. geminata* is clearly indicated by this mixture of characters (Muller, 1955). The present disposition of this entity as a variety of *Q. oleoides* is dictated by its somewhat greater richness in the characters of that species than in those of *Q. geminata*. Contrary to the opinion of Trelease, there is no indication of relation with *Q. virginiana* in any part of the insular population.

Specimens examined:

CUBA: Pinar del Rio: *N. L. Britton, E. G. Britton* and *J. F. Cowell* 9650, 10108; *N. L. Britton, E. G. Britton* and *C. S. Gager* 7304, 7305; *N. L. Britton* and *F. S. Earle* 6580; *M. T. Cook* 15, 16, 17, 18, 19, 20, 21, 22, *s. n.; F. S. Earle s. n.; V. Hermann* 813, 3324, 7561; *V. Hermann* and *Munz s. n.; E. P. Killip* 13564; *Bro. León* 4251; *Bro. León* and *Bro. M. Roca*

6990; *C. H. Muller* 9835, 9836, 9837, 9838, 9839, 9840, 9841, 9842, 9843, 9844, 9845, 9846, 9847, 9848, 9849, 9850, 9851, 9852, 9853, 9854, 9855, 9856, 9857, 9858, 9859, 9860, 9861, 9862, 9863, 9864, 9865, 9866, 9867, 9868, 9869, 9870, 9871, 9872, 9873, 9874, 9875, 9876, 9877, 9878; *O'Donovan* 1000; *W. Palmer* and *J. H. Riley* 432; *L. R. Rivas* 21996; *R. de la Sagra s. n.* (isotype of *Q. sagraeana* and *Q. cubana*); *J. A. Shafer* 11035, 11906, 11908, 11910; *J. A. Shafer* and *Bro. León* 13676; *C. Wright* 698, 2292.

REFERENCES

HARPER, R. M. 1913—Economic botany of Alabama. Part 1. Geographical report on forests. *Geol. Surv. Ala. Monogr.*, **8**. 222 p.

———1914—Geography and vegetation of northern Florida. *Florida State Geol. Surv. Ann. Report*, **6**: 163-437.

———1915—Vegetation types. *In* E. H. Sellards *et al.* The natural resources of an area in central Florida. *Florida State Geol. Surv. Ann. Report*, **7**: 135-188.

———1927—Natural resources of southern Florida. *Florida State Geol. Surv. Ann. Report*, **18**: 27-206.

———1928—Economic botany of Alabama. Part 2. Catalogue of the trees, shrubs, and vines of Alabama, with their economic properties and local distribution. *Geol. Surv. Ala. Monogr.*, **9**. 357 p.

MULLER, C. H. 1951a.—The significance of vegetative reproduction in *Quercus*. *Madroño*, **11**: 129-137.

———1951b.—The oaks of Texas. *Contr. Texas Research Found.*, **1**: 21-323.

———1955—The origin of *Quercus* on Cuba. *Rev. Soc. Cubana Bot.*, **12**: 41-47.

SARGENT, C. S. 1918.—Notes on American trees. I. *Quercus*. *Bot. Gaz.* **65**: 423-459.

SMALL, J. K. 1913.—*Flora of the Southeastern United States*. 2 ed. 1394 p. New York.

———1933—*Manual of the Southeastern Flora*. 1554 p. New York.

TRELEASE, W. 1924—The American oaks. *Mem. Nat. Acad. Sci.*, **20**. 255 p. 420 pl. (cf. pp. 112-116, pl. 189-202).

Normal Heteromorphism in Earthworms[1]

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ABSTRACT: Normally organized heteromorphic regenerates mentioned in the literature are of four species. Heteromorphic heads and tails from *Perionyx sansibaricus* and *Ocnerodrilus occidentalis*, as well as a heteromorphic tail from *Gordiodrilus peguanus*, are recorded. A heteromorphic head was developing at 47/48 on a specimen of the common lumbricid *Allolobophora tuberculata*. The pre-intestinal region is able, regardless of direction, to regenerate only a head or some portion of one. The intestinal region can regenerate heads as well as tails and at certain levels one or the other as determined by unknown factors of internal environment.

Anterior heteromorphism, a tail regenerated instead of a head, was discovered by Bonnet in oligochaetes (possibly including some earthworms) as long ago as 1745. Posterior heteromorphism, a head regenerated instead of a tail, was not recognized in earthworms until around 1925. Heteropolar growths may be monstrous in various ways, or a regenerate may be heteromorphic only in part and then also in different ways. Normal regenerates, *i.e.*, solely cephalic or caudal, with normal metamerism, and lacking outgrowths or other aberrations, have been recorded in the literature from four species of earthworms, as follows:

Criodrilus lacuum, European, with segments to 450. One heteromorphic head (Janda, 1926) of 16 segments at intersegmental furrow 22/23, a head of 20 and another of 23 segments at unknown levels. Heteromorphic tails rarely were obtained and then only from adults. No data were published as to kind of operation, level of regeneration or number of segments in regenerates. These heteropolar tails may have been produced by fragments with two cut surfaces as in *Eisenia foetida* or by short terminal portions as in species of *Perionyx*.

Eisenia foetida, of European origin but widely distributed in America, with 100-125 segments. Heteromorphic tails (Gates, 1949) regenerated at levels 20/21-54/55, number of segments increasing to a maximum of 25 at 40/41 and then decreasing. Heteromorphic tails (Gates, 1950b) also were regenerated by fragments of various sizes cut out from a middle portion of the body. Regeneration of heteromorphic heads (Gates, 1950a) is probable, in favorable conditions, at levels 16/17-34/35.

Perionyx excavatus, of Himalayan origin but now widely distributed in the tropics, with 100-200 segments. Heteromorphic head regeneration (Gates, 1927, 1941, 1943) possible at 12/13-27/28 and has been induced merely by a simultaneously made second transection at subsequent levels back to 68/69. Heteromorphic tails regen-

[1] From a manuscript written during tenure of a John Simon Guggenheim fellowship.

erated only by terminal portions comprising the last 42 or fewer segments. Data as to number of segments in heteropolar tails and in some of the heteromorphic heads no longer are available.

Perionyx millardi, endemic in peninsular India, with segments to 220. Heteromorphic heads regenerated at 7/8-22/23 (Gates, 1951) and after induction by a second transection at subsequent levels back to 88/89. Number of segments in these heteromorphs varied from 2-15, at 17/18 for instance and under uniform external conditions from 6-15, the maximum number obtained at several of the levels 17/18-31/32. Heteromorphic tails were regenerated by substrates comprising the last 44-17 segments, also by small fragments cut out from a posterior region of the body. Maximum number of segments 15, however usually only 1-5. All experimentally obtained regenerates in this species were provided by juvenile worms as adults were unobtainable. Heteromorphism occasionally found in natural regenerates was not normal.

Normal heteromorphism now can be recorded from three further species of earthworms. The procedures utilized have been described previously (Gates, 1927).

Perionyx sansibaricus, originally from peninsular India but now domiciled elsewhere in the tropics, with segments to 200. Heteromorphic heads regenerated at 7/8-20/21 and after induction by a simultaneous second transection at subsequent levels back to 50/51. Number of segments, 3 at 7/8, 6 and 8 at 8/9, 4-10 at 9/10, 7-15 at 20/21, 7-13 at 32/33. Heteromorphic tails were regenerated at levels 75/76-185/186, the substrates comprising the last 91-15 segments of the body. Number of segments, 2-8. Number of segments in heteromorphic tails regenerated by fragments cut out of the posterior portion of the body so as to contain the fifteen segments immediately in front of the last fifteen, 2-20. These results were obtained from operations on adult animals.

Gordiodrilus peguanus, peregrine and widely distributed in the tropics but presumably of African origin, possibly with 80-100 segments. One heteromorphic tail of 16+ segments at 16/17. Metameric differentiation had not been completed at time of preservation. The clitellum was still recognizable on segments xvii-xviii of the substrate and appeared to have undergone no regression during the two or more weeks required for formation of the regenerate.

Ocnerodrilus occidentalis, peregrine and widely distributed in temperate zones as well as in the tropics but presumably of American origin, with 70-84 segments. All regenerates from adults.

Heteromorphic heads of 6-7 segments regenerated at 19/20. Other posterior regenerates at the same level were cephalocaudal monstrosities or homomorphic tails. All posterior regenerates at levels 20/21-34/35 were normal homomorphic tails.

Heteromorphic tails at 21/22, at time of preservation, had not yet completed metameric differentiation though a number of segments already were demarcated and provided with setae. Other anterior

regenerates at 21/22 were monstrous. At 19/20 all anterior regenerates were monstrous, usually in part cephalic. All anterior regeneration at 12/13 was homomorphic. The maximum number of segments in those head regenerates was 10.

Worms of the above experiments had been fasted for a day or two before operating. Specimens of *O. occidentalis*, starved for several weeks before the operations, failed to regenerate though surviving long enough (3 weeks) to have done so.

Probability of normal heteromorphosis in another species of the same family as *E. foetida* also can be recorded.

Allolobophora tuberculata, of European origin but now widely distributed in other parts of the world, with 146-194 segments. A natural posterior regenerate at 47/48 might have become normally heteromorphic if development had been completed in the only direction that was morphologically recognizable. Unfortunately, feeding had continued after amputation and accumulations of ingested soil had ruptured the regenerate proximally just as the worm was found. Five segments already had been marked off externally on the regenerate. A pharyngeal bulb had been formed in the gut. The nerve cord terminated well away from distal end of regenerate in a subpharyngeal ganglion. The brain and circumpharyngeal commissures had not yet been formed. The distal end of the regenerate had the shape of a cephalic rather than a caudal growth but indications of prostomial sculpturing and buccal invagination had not become recognizable. The last two substrate segments had been considerably elongated. The epidermis and musculature had acquired a different appearance and texture indicative of histological changes. Setae of the 47th segment had been dehisced. Apertures of setal follicles had disappeared, leaving no recognizable traces of their former locations. Setal follicles apparently had been completely histolyzed. These are just the morphallactic changes sometimes associated, in better known species of earthworms, with head regeneration.

This regenerate, as well as the heteromorphic heads obtained at 32/33 and 34/35 in *E. foetida*, requires re-evaluation of results of various experiments on morphogenesis in earthworms. The regenerate also enables the following predictions. Homomorphic head regeneration will be obtainable, without special difficulty, in the pre-intestinal region of *A. tuberculata* and more rarely but only in conditions presently unknown at subsequent levels back to 47/48 at least. Equimeric heads will be regenerated at least at all levels back to 5/6, possibly even to 8/9 or 9/10.

DISCUSSION

Worms with heteromorphic regenerates are, of course, doomed to die from starvation or constipation unless some way is found to enable feeding or defecation. Although the enteric lumen is continuous from mouth to mouth in a two-headed individual, matter apparently can pass only in one direction, at least through a distal portion of the gut. Hence, ingesta accumulate until the mass is sufficient to rupture gut

and body wall. Even if the animal fasts, enteric secretions and especially calcareous concretions may burst out through substrate or regenerate. Individuals that were ruptured in the laboratory usually did not survive, even in hardy species with unusually high regenerative capacity. Greater viability in nature is not to be expected judging from rarity of heteromorphism in conditions resulting in frequent regeneration. Morphological regularization of heteromorphosis so as to permit feeding or defecation and presumably viability sometimes does take place, in nature as well as in the laboratory. The various sorts of regularization will be considered, circumstances permitting, in a subsequent communication.

Although only one kind of heteromorphism is known presently in two species, the other sort doubtless will be found. Heteropolar heads and tails have been found in six species of four families. Information as to heteromorphosis that is now available for four of the species warrants the following generalizations. The pre-intestinal region of the body, herein called head though that term sometimes has had a much more restricted meaning, is able to regenerate only a head or some portion of one. The intestinal region of the body is able to regenerate heads as well as tails and at certain levels one or the other as determined by unknown factors of internal environment. Similar regenerative capabilities are likely in the other four species.

REFERENCES

BONNET, C. 1745. Traité d'insectologie. Seconde partie. Paris.

GATES, G. E. 1927. Regeneration in a tropical earthworm, *Perionyx excavatus* E. Perr. *Biol. Bull.*, **53**:351-364.

———1941. Further notes on regeneration in a tropical earthworm, *Perionyx excavatus* E. Perrier, 1872. *J. Exptl. Zool.*, **88**:161-185.

———1943. Some further notes on regeneration in *Perionyx excavatus* E. Perrier. *Proc. Nat. Acad. Sci. India*, **13**:168-179.

———1949. Regeneration in an earthworm, *Eisenia foetida* (Savigny) 1826. I. Anterior regeneration. *Biol. Bull.*, **96**:129-139.

———1950. Regeneration in an earthworm, *Eisenia foetida* (Savigny) 1826. II. Posterior regeneration. III. Regeneration from simultaneous anterior and posterior transections. *Ibid.*, **98**:36-45; **99**:425-438.

———1951. Regeneration in an Indian earthworm, *Perionyx millardi* Stephenson. *Proc. Indian Acad. Sci.* (B), **34**:115-147.

———1953. On regenerative capacity of earthworms of the family Lumbricidae. *Am. Midl. Nat.*, **50**:414-419.

JANDA, V. 1926. Die Veränderung des Geschlechtscharakters und die Neubildung des Geschlechtsapparats von *Criodrilus lacuum* Hoffm. unter künstlichen Bedingungen. *Arch. Entwickmech. Org.*, **107**:423-455.

Early Development of the Secondary Bronchi in the House Sparrow Passer domesticus (Linnaeus)[1]

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ABSTRACT: This study presents the origin, development and relationships of the secondary bronchi in the embryo of the House Sparrow, *Passer domesticus (Linnaeus)*. Serial transverse, frontal or sagittal sections at six or eight microns were made of one or more embryos, fixed in Bouin's or Lavdowsky's fluid, embedded in paraffin and stained with Delafield's Hematoxylin, for each half-day interval from two through nine days incubation. Photomicrographs, camera lucida tracings, direct projections were used to make diagrammatic reconstructions at regular intervals of incubation.

The time and point of origin and general destination of each secondary bronchus is described. Three groups of secondary bronchi occur in this species. The five *mesiobronchi* arise on the dorsal, dorsomesial or dorsolateral surface of the mesobronchus and occupy the anteromesial and mesial regions of the lung. The nine *dorsobronchi* arise on the dorsal and dorsolateral surface of the mesobronchus and occupy the anterodorsal, dorsal and dorsolateral regions of the lung. The nine *lateroventrobronchi* arise on the lateroventral and lateral surfaces of the mesobronchus and occupy the ventral and lateroventral portions of the lung.

Detailed description is given for the development of the mesobronchus, secondary bronchi and tertiary bronchi concerned with the origin of the individual airsacs. Primary and secondary ostia of the intermediate and anterior abdominal airsacs are described. Migration of origins or mouths of secondary or tertiary bronchi from the lung to the airsac side of an airsac ostium are given for the intermediate, anterior abdominal and posterior abdominal airsacs.

The individual secondary bronchi are compared with those described in other species. The time of origin of the secondary bronchi in the House Sparrow are compared with those of the chicken; these structures appear earlier in the House Sparrow than in the chicken.

Introduction

Literature reviews on the structure of the respiratory system of Aves can be found in the works of Sappey (1847), Roche (1891), Baer (1896), Moser (1902), Bertelli (1905), Fischer (1905), Muller (1908), Schulze (1912), Juillet (1912), and Locy and Larsell (1916).

Selenka (1866) described the development of the airsacs in chickens. Locy and Larsell (1916) described in more detail the development of the lungs and airsacs in the domestic fowl. Bertelli (1905) and Poole (1909) discussed the diaphragmatic tissue in its relation to the development of the lungs and airsacs.

The present investigation describes the origin and location of

[1] Published in partial fulfillment of requirements for Ph.D. degree, University of Nebrask. ; University of Nebraska Department of Zoology Publ. No. 321.

the secondary bronchi in the embryo of *Passer domesticus* (Linnaeus), the house sparrow. The adult airsacs of this species have been figured grossly by such workers as Fischer (1905), Juillet (1912) and Wetherbee (1951).

Acknowledgments.—The writer expresses his thanks to his advisor, Dr. Otis Wade, Prof. Emeritus, University of Nebraska for guidance in this study. Acknowledgment is made to the North Dakota Institute of Regional Studies for financial support and to the Departments of Zoology and Veterinary Science for facilities used in this study.

MATERIALS AND METHODS

Embryos of the house sparrow were fixed in Bouin's fluid or Lavdowsky's fluid. Histological sectioning was performed using the dioxan-paraffin technique. Seventy per cent acid alcohol was used to soften older embryos. Serial sections of embryos were made at each half-day interval from two through thirteen days incubation (hatching time). Transverse, frontal and sagittal sections were used. Sections varied in thickness from six microns for the younger embryos to twenty microns for the embryos near and at hatching time. The lungs of several adults were sectioned between 10 and 20 microns. All staining was done with Delafield's hematoxylin.

Representative tracings and occasional photomicrographs from the various serially sectioned embryos were used in making diagrammatic reconstructions of the lungs, airsacs and airsac diverticula. Such reconstructions were made from frontal, lateral and mesial views.

OBSERVATIONS

The early stages of development of the lungs of the house sparrow are similar to that described for the chicken by Selenka (1866), Bertelli (1905), Poole (1909) and Locy and Larsell (1916) (Figs. 1, 2, 3, 4).

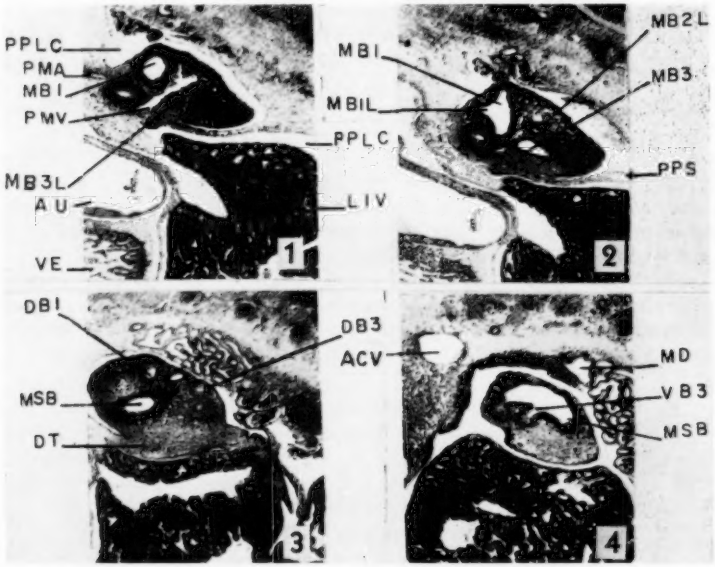
THE PRIMARY BRONCHUS

The primary bronchus enters the lung near its mesioventral apex. This bronchus is called the mesobronchus after it enters the lung (Huxley, 1882). A gradual shift of the entrance of the primary bronchus is apparent from three through nine days incubation. The final position of the point of entrance is the center of the mesial apex of the lung. The mesobronchus extends through the lung as a dorsolateroposterior continuation from its point of entrance. During the third day of incubation this tube becomes curved in three different regions: 1) the proximal end curves dorsoposteriorly and expands into the embryonic vestibulum; 2) the embryonic vestibulum projects sharply dorsally and laterally toward the dorsal floor of the lung; 3) the postvestibular mesobronchus turns sharply posteriorly and projects along the dorsolateral lung margin toward the posterior tip of the lung. This portion of the mesobronchus progressively diminishes in diameter from the embryonic vestibulum to the posterior limit of the mesobronchus which is curved mesially and ventrally (Fig. 5).

The posterior end of the mesobronchus pushes out of the lung slightly anterior to its posterior tip and ventral to its dorsal border by five days incubation. The projection of the mesobronchus beyond the lung wall into the pleuroperitoneal cavity constitutes the origin of the primordium of the *posterior abdominal airsac*.

THE SECONDARY BRONCHI

The primary bronchus of the embryo gives rise to twenty-three subdivisions of varying dimensions, the secondary bronchi. Each sec-



Figs. 1-4.—Sagittal sections of embryos of *Passer domesticus* at four and one-half days incubation; right lung sectioned at six microns; 100 magnifications. 1. Section through mesial area of lung showing entrance of pulmonary vein. 2. Section 50 microns lateral to Figure 1 showing entrance of primary bronchus into the lung. 3. Section 50 microns lateral to Figure 2 showing mesial extensions of dorsobronchi 1, 2, and 3. 4. Section 50 microns lateral to Figure 3 showing origins of lateroventrobronchi 2 and 3.

Abbreviations: ACV, anterior cardinal vein; AU, auricle; DB1, dorsobronchus number one; DB3, dorsobronchus number three; DT, diaphragmatic tissue; LIV, liver; MB1, mesiobronchus number one; MB1L, lateral ramus of mesiobronchus number one; MB2L, lateral ramus of mesiobronchus number two; MB3L, tertiary bronchus of mesiobronchus number three (MB3L is ICIM prior to the existence of the latter in the tissue outside the lung); MD, mesonephric duct; MSB, mesobronchus; PMA, pulmonary artery; PMV, pulmonary vein; PPLC, pleuroperitoneal cavity; PPS, pleuroperitoneal septum (synonym of diaphragmatic tissue); VB3, lateroventrobronchus number three; and VE, ventricle.

ondary bronchus, large or small, gives rise to subdivisions. The monopodial and dichotomous systems of branching of His (Locy and Larsell, 1916) are shown by the secondary bronchi in this species. This can be exemplified by a description of some of the ramifications of the most anterior secondary bronchus or first mesiobronchus. Numerous small subdivisions arise along the dorsal surface of the secondary bronchus in the monopodial fashion; the branches are smaller than the main trunk and are given off without a decrease in the size of the main trunk. Some of these tertiary bronchi are divided monopodially but many of them show bifurcations of equal dimension at their distal end. These quaternary bronchi originate in a dichotomous fashion. Subdivisions have been observed through the fifth and sixth order of bronchial branching. By the eleventh day of incubation the secondary, tertiary, quaternary, and lesser bronchi show a further subdivision in the form of small air capillaries which arise as projections from the secondary bronchi and other lesser bronchial subdivisions. Anastomoses of tertiary bronchi or bronchi of fourth, fifth or sixth order take place throughout the lung by the completion of ten days incubation. The more minute air passages also anastomose freely.

The secondary bronchi can be placed in three groups:

1. Mesiobronchi — bronchi which send tributaries over the mesial surface of the lung.
2. Lateroventrobronchi — bronchi which traverse the lateral and ventral area of the lung.
3. Dorsobronchi—bronchi which penetrate the lung mesoderm through most of the dorsal area of the lung.

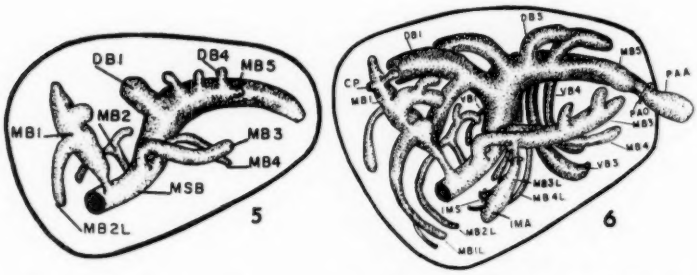
THE MESIOBRONCHI

The First Mesiobronchus (first entobronchus of Locy and Larsell, 1916).—This is the most anterior secondary bronchus and also the first to appear in the house sparrow in point of time. This secondary bronchus originates at about three days incubation as a projection from the dorsomesial surface of the mesobronchus immediately distal to the entrance of the primary bronchus into the lung (Fig. 5), and reaches the anterodorsomesial tip of the lung by three and one-half days incubation. At this time it has given off a large tertiary bronchus on its anteromesial margin about midway along the length of the secondary bronchus. This tertiary bronchus grows until it reaches the anteromesial border of the lung and then turns lateroventrally. By four and one-half days incubation the distal limit of this tertiary bronchus (the first lateroventral ramus) has reached its definitive position dorsal to the lateroventral apex of the lung and anteroventromesial to the lateroventral ramus of the second mesiobronchus (Fig. 6). An important quaternary bronchus arises at five days incubation on the lateroventral surface of the first lateroventral ramus and travels laterally and anteriorly to the lateroventral ramus. This quaternary

bronchus is the forerunner of the *lateral moiety* of the *interclavicular airsac*.

Numerous smaller tertiary bronchi appear along the dorsal and ventral surface of the secondary bronchus by six and one-half days incubation. All the tertiary bronchi of the first mesiobronchus occasionally divide dichotomously at their distal limits, but the more frequent method of subdivision is that of a lateral projection from the main axis of the bronchus (monopodial method). They develop quaternary subdivisions in monopodial and dichotomous fashion throughout their length.

At about five and one-half days incubation an anteriorly directed tertiary bronchus arises on the anterior surface of the first mesiobronchus a short distance proximal to the distal tip of the secondary



Figs. 5-6.—Diagrammatic reconstruction (mesial view) of bronchial ramifications in the right lung of embryos of *Passer domesticus* at various ages. 5. Four days incubation. 6. Five and one-half days.

Abbreviations: AAA, anterior abdominal airsacs; AASO, orifice of secondary ostium of anterior abdominal airsac; CA, cervical airsac; CAO, orifice of cervical airsac; CP, tertiary bronchus giving rise to cervical airsac; DB1, dorsobronchus number one; DB3, dorsobronchus number three; DB4, dorsobronchus number four; DB5, dorsobronchus number five; DB6, dorsobronchus number six; DB7, dorsobronchus number seven; DB9, dorsobronchus number nine; ICA, mesial moiety of interclavicular airsac; ICLMP, quaternary bronchus which originates lateral moiety; IMA, intermediate airsacs; IMS, secondary ostium of intermediate airsac; IMT, tertiary ostium of intermediate airsac; MB1, mesiobronchus number one; MB1L, lateral ramus of mesiobronchus number one; MB2, mesiobronchus number two; MB2L, lateral ramus of mesiobronchus number two; MB3, mesiobronchus number three; MB3L, tertiary bronchus of mesiobronchus number three (MB3L is ICIM prior to the existence of the latter in the tissue outside the lung); MB4, mesiobronchus number four; MB4L, lateral ramus of mesiobronchus number four; MB5, mesiobronchus number five; MSB, mesiobronchus; PAA, posterior abdominal airsac; PAO, orifice of posterior abdominal airsac; VB1, lateroventrobronchus number one; VB1A, anterior ramus of lateroventrobronchus number one; VB1V, ventral ramus of lateroventrobronchus number one; VB2V, ventral ramus of lateroventrobronchus number two; VB3, lateroventrobronchus number three; VB4, lateroventrobronchus number four; VB6, lateroventrobronchus number six; VB8, lateroventrobronchus number eight; and VB9, lateroventrobronchus number nine.

bronchus. This structure pushes against the lung wall and projects as a thumb-like bulge into the pleuroperitoneal cavity by six days incubation. This is the primordium of the *cervical airsac*.

The Second Mesiobronchus (second entobronchus of Locy and Larsell, 1916).—This structure arises between three and three and one-half days incubation as an anterodorsal projection from the dorsolateral surface of the mesobronchus immediately distal to the origin of the first mesiobronchus. The secondary bronchus bifurcates distally into two tertiary rami.

The mesioposterior ramus travels toward the mesial lung border where its distal end takes its place posterior to the most proximal of the mesioposterior tertiary bronchi of the first mesiobronchus. The ramus gives rise to tertiary bronchi in the same way and at the same time as does the first mesiobronchus.

The lateroventral ramus of the secondary mesiobronchus grows anteriorly, laterally and ventrally from its origin so that by five days incubation the distal end lies lateral, posterior and dorsal to the distal end of the lateroventral ramus of the first mesiobronchus.

The Third Mesiobronchus (third entobronchus of Locy and Larsell, 1916).—This bronchus originates during the fourth day of incubation as a dorsomesial projection from the mesial surface of the mesobronchus distal to the origin of the second mesiobronchus (Fig. 5). This branch turns sharply posteriorly and travels caudally along the mesial surface of the lung. Numerous large tertiary bronchi arise along the mesial surface and project dorsally and slightly posteriorly from four and one-half through seven and one-half days incubation. Another group of tertiary bronchi arises along the ventral surface. These project lateroventrally over the mesioventral surface of the lung. Additional smaller tertiary bronchi are noticed along the dorsal margin of the secondary bronchus. The third mesiobronchus gives rise to a mesioventrally directed projection (a tertiary bronchus) arising at approximately four days incubation on the ventromesial surface, a short distance posterior to the posteriorly directed curvature of the third mesiobronchus. By four and one-half days incubation this tertiary bronchus has reached the lung surface and, distal to this point, curves anterolateroventrally to a point ventral and lateral and slightly posterior to the origin of the parent secondary bronchus. By five days incubation the lateral surface of this tertiary bronchus shows a small projection (quaternary bronchus) midway along its length. During the following twelve hours the proximal and distal extremities of the tertiary bronchus remain in the lung while the entire middle portion and the proximal portion of the quaternary bronchus become located in the diaphragmatic tissue on the mesial surface of the lung; the tertiary bronchial portion outside the lung swells in diameter progressively from the proximal end. The distal portion of the tertiary bronchus now lying outside the lung is the *primordium* of the *mesial moiety* of the *interclavicular airsac* and the *intermediate* airsac. The primordium thus possesses a primary or proximal and a secondary or distal

ostium derived from the original tertiary bronchus plus a tertiary ostium or auxiliary connection derived from the laterally projected quaternary bronchus (Fig. 7).

The Fourth Mesiobronchus (fourth entobronchus of Locy and Larsell, 1916).—This structure arises at three and one-half days incubation as a projection from the anteromesial surface of the mesobronchus posterior to the origin of the third mesiobronchus. During the following twelve hours this branch turns dorsomesially and continues toward the mesial surface of the lung. This bronchus curves sharply posteriorly and travels lateroposteroventrally along the posterior portion of the mesial surface of the lung during the following two days incubation. The fourth mesiobronchus lies lateral and ventral to the posterior projection of the third mesiobronchus. Near its mouth, the fourth mesiobronchus gives rise to a ventrally directed tertiary bronchus which travels laterally and posteriorly to the similar tertiary bronchus of the third mesiobronchus.

The Fifth Mesiobronchus (the fifth ectobronchus of Locy and Larsell, 1916).—The fifth originates at about three and three-fourths days incubation as a mesioposterior projection from the mesial surface of the mesobronchus midway along the length of the posterior continuation, distal to the embryonic vestibulum. The secondary bronchus continues its growth posteriorly to the level of the three posterior lateroventrobronchi.

The fifth mesiobronchus is significant because the more posterior of

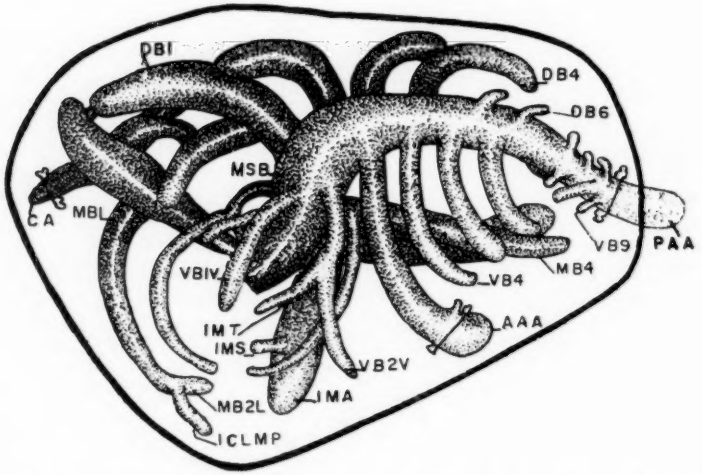


Fig. 7.—Diagrammatic reconstruction of bronchial ramifications in the left lung of an embryo of *Passer domesticus* after six days incubation; lateral view. For abbreviations see legend. Figs. 5 and 6.

the mesioposterior tertiary bronchi become associated with the distal ends of the three posterior dorsobronchi.

THE DORSOBRONCHI

The First Dorsobronchus (a ramus of the first ectobronchus of Locy and Larsell, 1916).—This structure originates by three and one-half days of incubation as a bulge on the anterior surface of the embryonic vestibulum immediately proximal to the posterior continuation of the vestibular region of the mesobronchus (Fig. 5). This secondary bronchus continues anterodorsomesially until it lies dorsal to the point of bifurcation of the second mesiobronchus; from this position, it turns anteriorly and slightly laterally as it grows along the dorsal floor of the lung. The final position of the distal or anterior tip is lateral, dorsal and slightly posterior to the distal limit of the first mesiobronchus.

The first dorsobronchus gives rise to a significant tertiary bronchus from its anteroventral margin, at the crest of the curvature described above, during the fifth day of incubation. This tertiary anterodorsomesial branch extends anterolateroventrally so that its subdivisions can anastomose with branches from the primordium of the lateral moiety of the interclavicular airsac by nine and one-half days incubation.

The Second Dorsobronchus (first ectobronchus of Locy and Larsell, 1916).—This bronchus originates by four days incubation as an anterodorsomesial protrusion from the anterodorsal surface of the mesobronchus distal to the origin of the first dorsobronchus. During the fifth day of incubation the second dorsobronchus curves dorsally and extends along the lateral surface of the anterior projection of the first dorsobronchus.

The Third Dorsobronchus (second ectobronchus of Locy and Larsell, 1916).—This structure appears during the fourth day of incubation on the dorsomesial surface of the mesobronchus posterior to the origin of the second dorsobronchus and on the opposite side of the mesobronchus from the origin of the third lateroventrobronchus. The third dorsobronchus projects toward the dorsomesial lung surface. It then turns posteriorly. The secondary bronchus comes to lie in its definitive position dorsomesial to the main mass of the fourth dorsobronchus during the sixth day of incubation.

The Fourth Dorsobronchus (third ectobronchus of Locy and Larsell, 1916).—The fourth originates at the same time as, and posterior to, the preceding dorsobronchus. The fourth dorsobronchus projects toward the dorsomesial surface of the lung and turns posteriorly to travel along the dorsal floor of the lung mesial to the mesobronchus and lateral to the posterior or distal continuation of the third dorsobronchus. Its distal limit lies dorsal to the distal extremity of the third mesiobronchus. The fourth dorsobronchus has no direct relation to the airsacs.

The Fifth Dorsobronchus (sixth ectobronchus of Locy and Larsell, 1916).—This bronchus appears at approximately six days incubation as a projection from the dorsolateral surface of the mesobronchus

posterior to the origin of the fifth mesiobronchus and dorsal to the origin of the sixth lateroventral bronchus. The fifth dorsobronchus turns posteriorly at the point where it approximates the dorsolateral margin of the lung and extends toward the posterior tip of the mesobronchus.

The Sixth Dorsobronchus (seventh ectobronchus of Locy and Larsell, 1916).—This structure originates at the same time and directly posterior to the fifth dorsobronchus. The growth and destination of the two bronchi are quite similar except for the fact that the sixth dorsobronchus does not extend as far posteriorly as the fifth dorsobronchus.

The Seventh Dorsobronchus.—This secondary bronchus has uncertain homology in the chicken as described by Locy and Larsell (1916). In the house sparrow, it originates by six days incubation on the dorsolateral surface of the mesobronchus proximal to the eighth and ninth dorsobronchi and extends dorsolaterally and anteriorly. The mouth or origin of the seventh dorsobronchus shif to the airsac side of the ostium of the posterior abdominal airsac.

The Eighth Dorsobronchus.—The eighth occurs on the dorsolateral surface of the mesobronchus posterior to the orifice of the seventh dorsobronchus; the two originate at the same time. The eighth dorsobronchus travels laterally and anteriorly along the dorsolateral margin of the lung until its distal end comes to lie adjacent to the distal end of a tertiary bronchus from the sixth dorsobronchus. The mouth of the eighth dorsobronchus shifts to the airsac side of the orifice of the posterior abdominal airsac (Fig. 8).

The Ninth Dorsobronchus.—The ninth originates on the dorsolateral surface of the mesobronchus, dorsal and distal to the orifice of

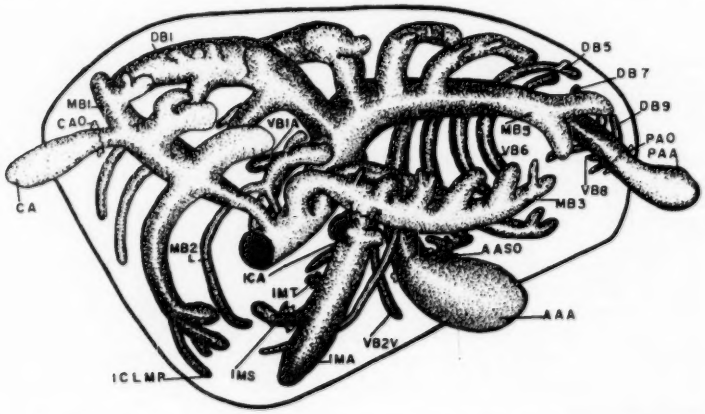


Fig. 8.—Diagrammatic reconstruction (mesial view) of representative tertiary and quaternary bronchi of right lung of an embryo of *Passer domesticus* at seven and one-half days incubation.

the preceding secondary bronchus, a few hours after the origin of the latter. The general destination of the ninth dorsobronchus is posterior, dorsal and slightly mesial to that of the eighth dorsobronchus. The mesial location is due to the curve in the mesobronchus proximal to the origin of the posterior abdominal airsac. The ostium of the ninth dorsobronchus precedes the ostia of the eighth and seventh dorsobronchi from the mesobronchus within the lung to the mouth of the airsac immediately outside the lung proper by the eleventh day of incubation.

The presence of the ostia of the three posterior dorsobronchi on the airsac mouth outside the lung by eleven days of incubation is similar and suggests a similarity to recurrent bronchi in other species (Juillet, 1912; Schulze, 1912; Locy and Larsell, 1916).

THE LATEROVENTROBRONCHI

The First Lateroventrobronchus (first laterobronchus of Locy and Larsell, 1916).—This structure arises at four days incubation on the anterolateral surface of the mesobronchus at the proximal limit of the embryonic vestibulum a short distance ventral and lateral to the origin of the first dorsobronchus. The structure bifurcates into a lateroventral and an anterolateral ramus by the completion of six days incubation. The former travels lateroventrally and slightly posteriorly until its distal end lies dorsal to the lateroventral margin of the lung. The latter lies dorsal, lateral and slightly posterior to the short second dorsobronchus and travels through the middle of the anterior portion of the lung. Both rami show subdivisions along their peripheries and at the distal limits by lateroventral ramus anastomoses with a quaternary bronchus from the secondary ostium of the intermediate airsac during the eleventh day of incubation.

The first lateroventrobronchus appears to be the homolog of the first laterobronchus of Locy and Larsell (1916); however, the anterior ramus is similar in general destination to the main trunk of the first dorsobronchus.

The Second Lateroventrobronchus (second laterobronchus of Locy and Larsell, 1916).—This and the preceding bronchus originate on the lateral surface of the anterior vestibular region at the same level and at the same time. Near its base it gives rise during the eighth day of incubation to a laterally projecting tertiary bronchus which subdivides sending quaternary branches to the lateral and dorsolateral margins of the lung. The secondary bronchus bifurcates distally during the sixth day of incubation to give rise to a ventral and an anterolateroventral ramus. The distal portion of the latter ramus anastomoses with the most posterior quaternary bronchus from the secondary ostium of the intermediate airsac by eleven days incubation.

The Third Lateroventrobronchus (third laterobronchus of Locy and Larsell, 1916).—This bronchus arises at four days incubation on the lateroventral surface of the mesobronchus immediately distal to

the point where the embryonic vestibulum curves posteriorly and begins to decrease in diameter (Fig. 6). It projects toward the lateroventral margin of the lung where, at five days incubation, the distal end curves sharply laterally, posteriorly and dorsally, and increases slightly in diameter.

The gradual expansion of the third lateroventrobronchus outside the lung establishes the *anterior abdominal airsac*. This airsac at first has a broad connection to the lung because of its origin from the subapical rather than the apical end of the secondary bronchus.

The entire curved expanded portion of the secondary bronchus near the lung surface lies outside the lung by seven days incubation. By nine days the apical end of the secondary bronchus has given rise to numerous tertiary bronchi within the lung. The anterior abdominal airsac by this time has increased its size in the diaphragmatic tissue so that the airsac is connected to the lung by means of a primary ostium (proximal portion of the original secondary bronchus) and a secondary ostium (distal portion or apical end of the original secondary bronchus).

The Fourth Lateroventrobronchus (the fourth laterobronchus of Locy and Larsell, 1916).—This structure originates at about eighty-four hours incubation as a projection from the ventrolateral surface of the mesobronchus directly posterior to the orifice of the preceding lateroventrobronchus and, like the latter, reaches the lateroventral margin of the lung in the adult. The general contour of the fourth is like that of the third. The curved distal end, however, does not bulge out of the lung as an airsac. The region proximal to the curve does not expand in diameter. A tertiary bronchus, arising near the base of the secondary, courses laterally toward the lung border and runs a course parallel to that taken by its counterpart from the third lateroventrobronchus.

The Fifth Lateroventrobronchus (the fifth laterobronchus of Locy and Larsell, 1916).—The fifth bronchus originates at six days incubation as a lateroventral projection from the mesobronchus posterior to the origin of the fourth lateroventrobronchus and by the seventh day of incubation reaches the lung margin.

This secondary bronchus is curved apically in a manner similar to but less distinct than the curvature of the preceding secondary bronchus in this group. The laterally projecting tertiary bronchus near the base of the secondary bronchus originates during the seventh day of incubation and travels a course parallel to that of its counterpart from the preceding secondary bronchus in this group.

The Sixth Lateroventrobronchus (the sixth laterobronchus of Locy and Larsell, 1916).—This structure originates at the same time as and posterior to the orifice of the preceding secondary bronchus in this group. The general growth and destination of this secondary bronchus follows that given for the fifth lateroventrobronchus.

The Seventh, Eight and Ninth Lateroventrobronchi.—These are

of doubtful homology to any secondary bronchus given by Locy and Larsell (1916).

The Seventh Lateroventrobronchus. — This secondary bronchus arises by six days of incubation as an anterolateroventral projection from the lateroventral surface of the mesobronchus immediately distal to the mesioventral curve in the posterior end of the mesobronchus. By nine days incubation it reaches its definitive position in the lung. The proximal portion of this secondary bronchus comes to lie in a plane parallel with that of the dorsal floor of the lung by the eleventh day of incubation. During the preceding day the mouth of this secondary bronchus becomes widened slightly and shifts its position from the mesobronchus to the airsac side of the ostium of the posterior abdominal airsac. That portion of the secondary bronchus which now lies outside the lung and makes a secondary connection between the lung and the airsac corresponds to a recurrent bronchus of previous authors.

The Eighth and Ninth Lateroventrobronchi. — These structures arise posterior to the seventh secondary bronchus in this group. The eighth lateroventrobronchus occurs anterior and dorsal to the ninth which lies on the lateroventral surface of the mesobronchus nearest the orifice of the posterior abdominal airsac. These two secondary bronchi have destinations similar to that given for the seventh lateroventrobronchus, and like it, their ostia become located on the airsac side of the ostium of the posterior abdominal airsac by the eleventh day of incubation.

DISCUSSION

The mesobronchus of the house sparrow shows much greater curvature immediately distal to the embryonic vestibular region than has been described for other species. The secondary bronchi in this species have been termed mesiobronchi, lateroventrobronchi, and dorsobronchi to give more accurate designation of their points of origin than is possible with earlier terminology. Huxley (1882) originated entobronchi to signify internal secondary bronchi. Locy and Larsell (1916) used entobronchi for the homologs of Huxley's entobronchi but used ectobronchi for the more anterior of the dorsally directed secondary bronchi from the vestibular and postvestibular region in the chick embryo. The use of the terms external and internal are likewise not sufficiently specific. Unlike Campana (1875) and Locy and Larsell (1916) no special consideration is deemed necessary for subdivisions of the secondary bronchi other than the use of the term *ramus* and the numerical treatment of successive tertiary bronchi from any given secondary bronchus. The consideration of certain tertiary bronchi as dorsobronchi by Locy and Larsell (1916) is not considered valid because such branches are not secondary bronchi but tertiary bronchi. The term secondary bronchus is restricted to a bronchus originating on the mesobronchus. This definition is in distinction to the minute air capillaries that are observed in later embryology. Table I compares the individual secondary bronchi of the house sparrow with the

TABLE I.—Comparison of terminology of secondary bronchi

House Sparrow (present paper)	Duck (Sappey, 1847)	Chicken (Campana, 1875)	Duck and Apteryx (Huxley, 1882)	Chicken (Locy and Larsell, 1916
Mesiobronchus No. 1	Diaphragmatic No. 1	Divergent No. 1	Entobronchus No. 1	Entobronchus No. 1
Mesiobronchus No. 2	Diaphragmatic No. 2	Divergent No. 2	Entobronchus No. 2	Entobronchus No. 2
Mesiobronchus No. 3	Diaphragmatic No. 3	Divergent No. 3	Entobronchus No. 3	Entobronchus No. 3
Mesiobronchus No. 4	Diaphragmatic No. 4	Divergent No. 4	Entobronchus No. 4	Entobronchus No. 4
Mesiobronchus No. 5	Costal No. 6	Internal No. 5	Ectobronchus **	Ectobronchus No. 5
Dorsobronchus No. 1	Costal No. 1	Internal No. 1	Ectobronchus **	Ectobronchus No. 1
Dorsobronchus No. 2	Costal No. 2	Internal No. 2	Ectobronchus **	Ectobronchus No. 1
Dorsobronchus No. 3	Costal No. 3	Internal No. 3	Ectobronchus **	Ectobronchus No. 2
Dorsobronchus No. 4	Costal No. 4	Internal No. 4	Ectobronchus **	Ectobronchus No. 3
Dorsobronchus No. 5	Costal No. 5	Internal No. 6	Ectobronchus **	Ectobronchus No. 4
Dorsobronchus No. 6	Costal No. 7	Internal No. 7	Ectobronchus **	Ectobronchus No. 6
Dorsobronchus No. 7	Costal **	Internal **	Ectobronchus **	***
Dorsobronchus No. 8	*	*	*	***
Dorsobronchus No. 9	*	*	*	***
Lateroventrobronchus No. 1	*	*	*	Laterobronchus No. 1
Lateroventrobronchus No. 2	*	External No. 1	*	Laterobronchus No. 2
Lateroventrobronchus No. 3	Branch of Mesobronchus	External No. 2	Branch of Mesobronchus	Laterobronchus No. 3
Lateroventrobronchus No. 4	*	External No. 3	*	Laterobronchus No. 4
Lateroventrobronchus No. 5	*	External **	*	Laterobronchus No. 5
Lateroventrobronchus No. 6	*	External **	*	Laterobronchus No. 6
Lateroventrobronchus No. 7	*	*	*	***
Lateroventrobronchus No. 8	*	*	*	***
Lateroventrobronchus No. 9	*	*	*	***

* Bronchial group not described.
** Bronchial group described but homology not certain.
*** Homology of bronchial groups not determined.

probable homologs in other species as described by previous workers.

Special attention must be called to certain features of the house sparrow. The anterior four mesiobronchi are undoubtedly the homologs of the first four secondary bronchi described in other groups as arising distal to the entrance of the primary bronchus into the lung. The fifth mesiobronchus, though it arises from the posterior third of the mesobronchus, occupies the mesial, posterior area of the lung and thus fits into the group here termed mesiobronchi. On the basis of the actual secondary bronchi in the chicken as described by Locy and Larsell (1916), the number of true dorsobronchi from the posterior region of the mesobronchus in the chicken is greater than in the house sparrow. The number of entobronchi and mesiobronchi are the same except for the fifth mesiobronchus which corresponds to their fifth ectobronchus.

The number of dorsobronchi from the vestibular and immediate postvestibular region in the house sparrow is the same as the number of ectobronchi in the chicken except for the first and second dorsobronchi which are the apparent homologs of the branch and the main

TABLE II.—Time of origin of secondary bronchi

House Sparrow	Days of Incubation	Chicken (Locy and Larsell, 1916)	Days of Incubation
Mesiobronchus No. 1	3	Entobronchus No. 1	5¼
Mesiobronchus No. 2	3½	Entobronchus No. 2	5½
Mesiobronchus No. 3	3½	Entobronchus No. 3	5½
Mesiobronchus No. 4	3½	Entobronchus No. 4	6
Mesiobronchus No. 5	3¾	Ectobronchus No. 5	*
Dorsobronchus No. 1	3½	Branch of Ectobronchus No. 1	6
Dorsobronchus No. 2	3	Ectobronchus No. 1	6
Dorsobronchus No. 3	3½	Ectobronchus No. 2	6
Dorsobronchus No. 4	3½	Ectobronchus No. 3	*
Dorsobronchus No. 5	6	Ectobronchus No. 4	*
Dorsobronchus No. 6	6	Ectobronchus No. 6	**
Dorsobronchus No. 7	6	***	
Dorsobronchus No. 8	6	***	
Dorsobronchus No. 9	6	***	
Lateroventrobronchus No. 1	4	Laterobronchus No. 1	6
Lateroventrobronchus No. 2	4	Laterobronchus No. 2	6
Lateroventrobronchus No. 3	4	Laterobronchus No. 3	6
Lateroventrobronchus No. 4	4	Laterobronchus No. 4	**
Lateroventrobronchus No. 5	5½	Laterobronchus No. 5	**
Lateroventrobronchus No. 6	5½	Laterobronchus No. 6	**
Lateroventrobronchus No. 7	6	***	
Lateroventrobronchus No. 8	6	***	
Lateroventrobronchus No. 9	6	***	

* Exact time not stated; figures show structure by end of seventh day.
** Exact time not stated; figures show structure by end of eighth day.
*** Homology not determined.

stem of the first ectobronchus in the chicken. The last three dorsobronchi in the house sparrow may correspond to recurrent bronchi of the posterior abdominal airsacs figured by Juillet (1912), Schulze (1912), Locy and Larsell (1916), or to the posterior dorsobronchi in the White Pekin duck described by Delphia (1958).

The first lateroventrobronchus in the house sparrow represents a possible intergrade between the lateroventrobronchi and the dorsobronchi. The destination of its anterior ramus is in the most ventral, anterior region that is occupied by the anterior projection of the first dorsobronchus. The third lateroventrobronchus (origin of the anterior abdominal airsac) in the house sparrow is not only the homolog of the laterobronchus number three in the chicken (Locy and Larsell, 1916) but undoubtedly the homolog of the "branch" of the mesobronchus in *Apteryx* cited by Huxley (1882) for the origin of the equivalent of the anterior abdominal airsac. It has been observed (Delphia, 1958) that the third laterobronchus in the duck is the homolog of the third laterobronchus of the chicken (Locy and Larsell, 1916). The three posterior lateroventrobronchi in the house sparrow are possible homologs of the lateroventral groups of recurrent bronchi of the posterior abdominal airsac figured for numerous species by Juillet (1912) and Schulze (1912) and for the chicken by Locy and Larsell (1916), or they are the homologs of the posterior laterobronchi in the White Pekin duck (Delphia, 1958).

Locy and Larsell (1916) give the only complete description of the development of the secondary bronchi. Table II compares the time of origin of the secondary bronchi in the house sparrow (an altrial bird with a thirteen-day incubation period) with the apparent homologs in the chicken (a precocial bird with a twenty-one day incubation period).

The secondary bronchi in the house sparrow appear and develop earlier than in the chicken. This is in contrast to the redwing, *Aegeleus phoniceus* (Linneaus) in which only eight secondary bronchi have been found by six days incubation (Daniel, 1957). The redwing and the house sparrow both have fewer secondary bronchi than the chicken.

SUMMARY

The time of origin, point of origin and general destination of each secondary bronchus is described for the house sparrow. Detailed description is given for the development of the mesobronchus, secondary bronchi and tertiary bronchi concerned with the origin of the individual airsacs. Primary and secondary ostia of the intermediate and anterior abdominal airsacs are described. Migration of origins or mouths of secondary or tertiary bronchi from the lung to the airsac side of an airsac ostium are given for certain airsacs.

The individual secondary bronchi are compared with those described in other species. The time of origin of the secondary bronchi in the house sparrow are compared with those of the chicken.

REFERENCES

BAER, MAX. 1896. Beitrag zur Kenntnis der Anatomie und Physiologie der Athemwerkzeuge bei den Vogeln. *Zeitschr. Wiss. Zool.*, **61**:420-498.

BERTELLI, DANTE. 1905. Richerche di embriologia e di anatomia comparata sul diaframma e sull' apparechio respiratorio dei vertebrati. *Arch. Italiano Anat. Embriol.*, **4**:593-633; 776-844.

CAMPANA, ARTERE. 1875. *Physiologie de La Respiration chez Les Oiseaux.* Anatomie de l'appareil pneumatique pulmonaire, des faux diaphragmes des sereuses et de intestine chez le Poulet. Masson, Paris. 385 pp.

DANIEL, J. D., JR. 1957. An embryological comparison of the domestic fowl and the redwinged blackbird. *Auk*, **74**(3):340-358.

DELPHIA, J. M. 1958. The origin of the airsacs in the White Pekin duck, *Anas platyrhrynchos* Linnaeus. *Proc. North Dakota Acad. Sci.*, **12**: 86-92.

FISCHER, G. 1905. Vergleichend-anatomische Untersuchungen über den Bronchialbaum der Vogel. *Zoologica Stuttgart*, **19**:1-45.

HUXLEY, T. H. 1882. On the respiratory organs of *Apteryx*. *Proc. Zool. Soc. Lond.*, **21**:560-569.

JUILLET, ARMAND. 1911-12. Recherches anatomiques, embryologiques, histologiques et comparatives sur le poumon des Oiseaux. *Arch. Zool. Exptl. et Gen.*, **9**:207-371.

LOCY, W. A., AND OLOF LARSELL. 1916a. Part 1. The embryology of the bird's lung. *Am. J. Anat.*, **19**:447-504.

———1916b. Part 2. The embryology of the bird's lung. *Ibid.*, **21**:1-44.

MOSER, FANNY. 1902. Beitrage zur vergleichenden Entwicklungsgeschichte der Wirbeltierlunge. *Arch. Mikr. Anat.*, **60**:587-667.

MULLER, BRUNO. 1908. The airsacs of the pigeon. *Smithsonian Misc. Col.*, **50**: 365-414.

POOLE, M. 1909. The development of the subdivisions of the pleuroperitoneal cavity in the birds. *Proc. Zool. Soc. Lond.*, **49**:210-235.

ROCHE, G. 1891. Contribution a l'etude de l'anatomie comparee des reservoirs aeriens d'origine pulmonaire chez les oiseaux. *Ann. Sci. Nat.*, **11**(7): 1-120.

SAPPEY, P. C. 1847. *Recherches sur l'Appareil Respiratoire des Oiseaux.* Germer-Bailliere, Paris. 92 pp.

SCHULZE, F. E. 1912. Über die Luftsacke der Vogel. *Verh. Interm. Zool. Kong. Graz*, **8**:446-482.

SELENKA, EMIL. 1866. Beitrag zur Entwickelungsgeschichte der Luftsacke des Huhnes. *Z. Wiss. Zool.*, **16**:178-182.

WETHERBEE, DAVID K. 1951. Airsacs in the English Sparrow. *Auk*, **68**(3): 242-244.

Ecological Relationships Between Vegetation and the Distribution of Land Snails in Montana, Colorado and New Mexico

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ABSTRACT: Thirty-two species and subspecies of shelled land mollusks were collected. Ninety-nine per cent of the snails were associated with some form of deciduous tree, usually aspen. Food chain relationships between aspen and land snails appear likely. The amount of available calcium also is a factor noted to be related to vegetation and affecting snail distribution. Because of these relationships, it is proposed that snail distribution be reported in terms of associated vegetation rather than altitude. Snail distribution in burned areas is also discussed. Chance distribution appears unlikely to be the only method involved and small, permanent populations within conifers are suggested to occur. *Vertigo gouldi arizonensis*, *Gastrocopta pilsbryana* and *Striatura meridionalis* are reported as new records for the state of Colorado.

Land areas are often characterized by their dominant vegetation since the trees and plants which cover an area are easily seen and recognized by even a casual observer. This is particularly true in the mountainous regions of the western United States where the various plant formations are frequently composed almost exclusively of one or two tree species and where the boundary lines between major formations are often clearly defined as a result of physiographic and ecological factors. That the distribution of the plants may be expected to have a marked influence upon the distribution of land mollusks is self-evident although some discussion of the mechanisms involved is presented here. It is strongly suggested that future molluscan records be reported in terms of the vegetation of the collecting site instead of the altitude as is frequently done. Obviously the environment at 10,000 feet at Santa Fe, New Mexico, the southernmost point of the area investigated, differs markedly from that at the same altitude in Glacier National Park, Montana, the northernmost point of investigation. Opposing slopes on a single mountain are often covered by conspicuously different vegetation as a result of exposure to wind and snow, varying amounts of insolation and other ecological factors. To be meaningful, altitude records for snails must be adjusted since latitude and local conditions prevent direct comparisons, while reports including observations of vegetation are immediately comparable.

Correlations between 15 major plant associations and the occurrence of various species of land snails are discussed in this paper. Field work was carried on in Colorado and north-central New Mexico during the summer of 1958, supported by grant number 228-J of the

TABLE I.—The number of snails collected in each of 15 vegetation types

	Types of Associations															
	Deciduous			Deciduous-Coniferous				Coniferous					Other			
	Quaking Aspen	Deciduous Chapparal	Mixed Deciduous	Mixed Deciduous-Coniferous	Lodgepole Pine-Quaking Aspen	Engelmann Spruce-Quaking Aspen	Engelmann Spruce-Lodgepole Pine-Aspen	Piñon Pine-Juniper	Ponderosa Pine	Lodgepole Pine	Engelmann Spruce-Alpine Fir.	Limber Pine	Grasslands	Sage-Cactus-Yucca	Lichen-Moss	Total
Number of Stations	17	2	6	6	6	3	1	7	2	3	5	1	7	2	4	72
Oreohelix subrudis	6		53	3			3									65
Oreohelix sp.	1				2											3
Ashmunella ashmuni				33												33
Euconulus fulvus alaskensis	84		7	15	25		5						1			137
Retinella electrina	13			5			1									19
Retinella binneyana occidentalis	2				2											4
Retinella sp.				1												1
Hawaii miniscula							1									1
Zonitoides arboreus	47		73	108	28		11			1						268
Striatura meridionalis					1											1
Vitrina alaskana	44		4		11	3	3									65
Discus cronkhitei	89		29		41								15			174

TABLE I.—(continued)

Discus shimeki cockerelli	5		5	141	5	20	5										181
Punctum minutissimum	1																1
Succinea avara	6				1												7
Succinea grosvenori						2											2
Pupillidae	4		2				2			2							10
Gastrocopta pilsbryana					15												15
Gastrocopta pilsbryana amissidans							1										1
Pupilla cf. hebes	1																1
Pupilla blandi	140		2	99	67		22										330
Pupilla muscorum	7				16			1									24
Vertigo concinnula	10		10	5	7	1											33
Vertigo gouldi arizonensis					11		7										18
Vertigo gouldi basidens	2																2
Vertigo ovata			7														7
Vertigo modesta parietalis	4				2	7	6										19
Columella edentula	2				1												3
Vallonia cyclophorella	89			80	25					1							195
Vallonia albula			1														1
Vallonia gracilcosta	3				25		89										117
Vallonia sp.	4			1	1												6
Zoogenetes harpa	137						3										140
Cionella lubrica	10		1	1	2		1										15
Unknowns	3		3		1												7
Total	714	0	197	492	289	33	158	3	0	4	0	0	16	0	0		1906

American Philosophical Society. Supplementary investigations in Montana during the summer of 1959 were supported by a grant from the Society of Sigma Xi.

Collecting stations were established in Mesa Verde, Glacier and Rocky Mountain National Parks. The writer wishes to thank the superintendents and staffs of those parks for their cooperation.

Most collections were made at scattered points in the mountainous portions of Montana, Colorado, and New Mexico. Seventy-two stations were sampled in the latter two states. These stations ranged in altitude from 5,500 to 12,300 feet and are the ones included in the data in Table I. Less extensive collections, made in Montana, are not included in the tabular material although the discussion does include such data.

Each station represented an area of less than 200 square yards in which an intensive search was made for mollusks. Collections were not made within a given period of time or over a specified area. The greatest amount of time was spent at those stations which were most productive. Such methods yielded the largest number of specimens for taxonomic study, a primary purpose of this investigation, but rendered impossible the application of some types of statistical analysis to the data.

ECOLOGICAL DISCUSSION

Fifteen distinct plant associations were recognized and are listed in Table I. The common names which are used following Harrington (1954). The presence of deciduous trees is closely linked to the distribution of western land mollusks. Forty-eight per cent of the snails were collected at 25 stations in deciduous plant associations. Virtually all of the other snails were collected at another 16 stations where deciduous trees represented a significant fraction of the dominant vegetation. Thus, 99 per cent of the entire number of snails collected were found at 44 stations, or only 57 per cent of the total number of stations. The single species of deciduous tree present at almost all of these stations was quaking aspen, *Populus tremuloides*. This association between aspen and snails may be related to the source of organic residues in the soil. Burch (1955) showed a correlation between the amount of organic matter which plants supplied to the soil and the distribution and abundance of snails in eastern forests, and a similar correlation is likely to exist in the west. It is also probable that aspen leaves or molds and fungi growing upon fallen aspen are directly associated with snails in a food chain relationship.

It is well known that the pH of soil is strongly influenced by the type of vegetation growing upon the soil. Conversely, pH may also limit the plants which can grow in a particular area. In general, coniferous forests are found upon acid soils. Deciduous forests may be found in alkaline areas but are not necessarily restricted to them. A small number of pH readings were made of the soil at various collecting sites. A difference of only 0.4 existed between the soil pH

beneath aspens where snails were present and the soil pH beneath lodgepole pine where no snails were found. Both stand of trees were growing on the same glacial moraine and were adjacent to each other. It is unlikely that the slight differences observed in the pH are responsible for the differences in the snail populations and it would be inaccurate to consider soil pH as a major factor in determining the distribution of snails, although this occasionally has been done. Of greater significance is the availability of calcium. Karlin (1956) has shown that numerous snails occurred in greenhouses where acid soils were found. In those soils, high levels of soluble calcium were produced by extensive fertilization. Joffee (1949) indicated that large quantities of calcium are returned to the soil by decomposing leaves and logs where it may form an insoluble Ca-humate upon drying. Snails which are able to utilize either soluble or insoluble calcium might survive in areas of acid soil. Records (Van Cleave, 1959) indicate that snails of several species are seasonally abundant in the acid duff of Mesa Verde National Park, where limestone outcroppings are unknown and where the dominant trees are conifers, pinon pine and juniper. It would appear that Oosting's statement (1950), "With such a variety of things that may be affected by soil acidity, it should be suspected that a simple relationship between pH and plant responses does not exist . . . pH alone cannot be the limiting factor," is justified for snails as well as plants.

An interesting problem is presented by the almost complete absence of snails from the coniferous forests which were studied. If snails are most frequently associated with aspen, a tree which follows fires in the pine, spruce, and fir forests of the region investigated, where do the snails originate? Heyward and Tissot (1936) have shown the ability of soil organisms to survive in burned-over areas, although their numbers are significantly reduced. The most likely speculation is that populations of snails, too small to be readily detected, are always present in coniferous areas. Careful sampling at 18 stations would indicate that such is not the case, however. A total of only seven snails was found at two stations in pine woodlands while not a single snail could be located in the spruce-fir forests. Isolated stands of aspen within large stands of spruce and fir invariably had snail faunas.

Possible distribution by birds and other animals apparently cannot account for all of the snail colonies which arise in new stands of aspen. Adventitious or accidental transport of snails into recently burned areas involves what Baker (1958) referred to as small number chance based solely upon luck. One snail species might even be expected to be distributed over a relatively small area within reasonable periods of time on such a chance basis, but this does not satisfactorily explain the presence of many species in almost all aspen woods.

Burned areas were visited in Glacier National Park, Montana, twenty-three years after the fire. Living snails were found associated with burned stumps of alpine fir and the Engelman spruce which

were being replaced by lodgepole pine and aspen. Burns only five and seven years old were also visited. No snails were found in those areas although replacement by lodgepole pine, aspen and larch was well initiated. An apparently recent burn of aspen, date of burning unknown, was found to contain a number of species and individuals of living snails. This latter observation suggests that snails can and do survive fires since it is likely that the aspen contained snails prior to burning. No conclusions can be drawn concerning the presence of snails in what formerly were coniferous woods. Despite the lack of evidence now available, it appears most logical to assume that very small snail populations do exist in most coniferous woods until fire-produced changes in the environment permit a rapid population increase.

MOLLUSCAN SPECIES COLLECTED

A total of 32 species and subspecies of land snails were collected. Slugs are not included in the list of species given in Table I, since they will be the subject of a separate paper. All scientific names in Table I follow Pilsbry (1939-1948).

Three of the species are new records for the state of Colorado. The ranges of many other species reported by Henderson (1907, 1924, 1936) and Pilsbry (1939-1948) have been extended.

Thanks are offered to Dr. Henry van der Schalie for assistance in identifying or checking some of the molluscan material. Examples of all the species collected have been deposited in the author's collection and/or that of the Museum of Zoology of the University of Michigan.

Some notes of particular interest follow:

A single individual of *Striatura meridionalis* was found in the Graham Creek campground on the east shore of Lake Vallecito near Durango, Colorado, thus representing a new record for the state. It was associated with several other species of snails in a mixed forest of lodgepole pine and quaking aspen.

Two individuals of *Succinea grosvenori* were collected in Mesa Verde National Park, Colorado. Both were found in sandy exposed situations in piñon pine and juniper forests. However, both snails were found within 6 feet of permanent streams, thus suggesting that the micro-habitats may not have been the extreme xeric ones indicated by Shimek (1935) for this species.

Fifteen individuals of *Gastrocopta pilsbryana* were collected at two stations on the east shore of Lake Vallecito near Durango, Colorado. These apparently represent the first records for this species in Colorado, although it is reportedly distributed abundantly in New Mexico not far to the south. There are also records from Utah to the west, thus suggesting that future finds may show a continuous distribution in suitable areas throughout southern Colorado. Both stations were characterized by a lodgepole pine-quaking aspen association. One typical individual of *Gastrocopta pilsbryana amissidens*

was collected together with *pilsbryana* proper. Since modern genetic concepts do not allow for synpatry, it is suggested that *amissidens* may not be a valid subspecies but only a variant.

Eighteen individuals of *Vertigo gouldi arizonensis* were collected on the east shore of Lake Vallecito near Durango, Colorado. This is still another new state record to come from that area. The previous distribution records for this species and others found with it at Lake Vallecito suggest that the fauna of the area has strong affinities to that of the mountains of New Mexico, 100 miles or more to the south.

Columella edentula was found in both northern and southern Colorado although only three individuals were collected, one at each of three localities. Pilsbry (1948) does not include Colorado in the known range of this northern species. However, he suggests that some of the Colorado records for *C. alticola* (Ingersoll) might actually refer to this species. Henderson (1924) does include two Colorado records for *C. edentula*. It is likely that this species occurs sporadically in the mountains much further south than previously suspected.

Zoogenetes harpa is a boreal species extending southward only at high elevations. Colorado localities near the 40th parallel represent the southernmost limit of its reported range (Pilsbry, 1948). Three individuals were found during this study at Lake Vallecito in southern Colorado, thus extending the known range of this species approximately 200 miles further south.

REFERENCES

BAKER, H. BURRINGTON 1958. Land snail dispersal. *Nautilus*, **71**:141-147.

BURCH, JOHN B. 1955. Some ecological factors of the soil affecting the distribution and abundance of land snails in eastern Virginia. *Ibid.*, **69**:62-69.

HARRINGTON, H. D. 1954. *Manual of the Plants of Colorado*. Sage Books, Denver. 666 pp.

HENDERSON, JUNIUS 1907. The Mollusca of Colorado, I. *Univ. of Colo. Studies*, **4**:77-96.

———1924. Mollusca of Colorado, Utah, Montana, Idaho and Wyoming. *Ibid.*, **13**:65-223.

———1936. Mollusca of Colorado, Utah, Montana, Idaho and Wyoming — supplement. *Ibid.*, **23**:81-145.

HEYWARD, FRANK AND A. N. TISSOT 1936. Some changes in the soil fauna associated with forest fires in the longleaf pine. *Ecology*, **17**:659-666.

JOFFEE, JACOB S. 1949. *Pedology*. Somerset Press, New Brunswick. 602 pp.

KARLIN, EDWARD J. 1956. Notes on the ecology of *Zonitoides arboreus* (Say), *Opeas pumilum* (Pfeiffer) and *Lamellaxis gracilis* (Hutton) in greenhouses. *Am. Midl. Nat.*, **55**:121-125.

OOSTING, HENRY J. 1950. *The Study of Plant Communities*. Freeman and Co., San Francisco. 389 pp.

PILSBRY, HENRY A. 1939-1948. Land Mollusca of North America. *Acad. Nat. Sci. Phil. Monograph*, **3**: Vol. I, 994 pp. Vol. II, 1113 pp.

SHIMEK, B. 1935. The habitats of Iowa succineas. *Nautilus*, **49**:6-10.

VAN CLEAVE, PHILIP F. 1959. Personal communication.

Factors Influencing the Local Distribution of Shrews

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ABSTRACT: A field study was made of the factors influencing the local distribution of *Sorex cinereus* and *Blarina brevicauda* in southern Michigan. The environmental factors considered were vegetation type, cover (fallen trees, brush, leaf litter), temperature, food, moisture and interspecific competition. *Blarina brevicauda* was found only in moist situations but avoided standing water. It was scarce or absent in those habitats in which the available food supply (consisting of the larger forms of invertebrates) was low. Vegetation, type of cover, temperature, and interspecific competition were not important factors. *Sorex cinereus* occurred in all habitats except upland hardwoods. The reason for the avoidance of this habitat was not determined, but it apparently was not a response to the type of vegetation. *Sorex* was relatively less abundant in the drier situations than was *B. brevicauda* and did not avoid standing water. *S. cinereus* may be able to utilize smaller food items (collembolans, ants, spiders) than *B. brevicauda*, so that its local distribution is not influenced by the availability of the larger invertebrates. Type of cover, temperature, and interspecific competition were not important factors in its local distribution.

Shrews have been found to normally inhabit moist situations (Pruitt, 1953, 1959; Manville, 1949; Wetzel, 1958). Such a restriction to moist areas most likely results from a large turnover of water by shrews (Chew, 1951). Pruitt (*op. cit.*) has further analyzed the physical factors influencing the local distribution of shrews and found both temperature and moisture to be important factors. The relative importance of the various biotic factors (i.e., food availability, vegetation type, and interspecific competition) have not been thoroughly investigated. Pearson (1947) has shown that shrews have high metabolic rates and as a result require large intakes of food. As a result one might expect the availability of food to play an important role in the local distribution of shrews.

The present paper contains data pertaining to the masked shrew, *Sorex cinereus*, and the shorttailed shrew, *Blarina brevicauda*, obtained during a study of the factors influencing the local distribution of small mammals in southern Michigan. Data concerning other species will be presented elsewhere (*Microtus pennsylvanicus* and *Synaptomys cooperi*, in press; *Peromyscus leucopus* and *Zapus hudsonius*, in preparation). Most of the habitats studied had conditions moist enough to be considered favorable in regard to this factor. Shrews did not occur in all study areas, however; it was desired, therefore, to determine the factors influencing distribution within these moist areas.

Acknowledgments.—The material presented here represents a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the University of Michigan. I am grateful to Drs.

W. H. Burt, W. S. Benninghoff, F. C. Evans, and H. van der Schalie for their assistance and encouragement during the course of the study. I wish also to thank my wife, Mary Ruth, for doing many of the compilations. The field work was done under the auspices of a Horace H. Rackham predoctoral fellowship.

DESCRIPTION OF THE STUDY AREA

All work was done on the University of Michigan's Mud Lake Research Area, located in northern Washtenaw County, Michigan. The study consisted essentially of three parts: (1) a generalized study of seven habitats (old field, marsh, bog mat, hardwood swamp, oak-hickory upland, spruce swamp, and spruce burn); (2) a more intensive study of the old field and marsh; and (3) studies along a series of transects. A description of the seven habitats and transects is given below (plant nomenclature follows that of Fernald, 1950). Complete vegetative descriptions and phytosociological tables are not given for the marsh, old field, and bog mat; these are published elsewhere (Getz, 1959).

Old Field.—A field abandoned for approximately 15 years. The vegetation consists primarily of *Poa compressa*, *Potentilla intermedia*,

TABLE I.—Partial Braun-Blanquet relevés from the swamp hardwoods. A, from the wet portion; B, from the moist portion. The numbers indicate abundance-cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Relevé A	Relevé B
Tree stratum		
Acer rubrum	3.1	4.1
Ulmus americana	3.1	+.1
Betula lutea	+.1	2.1
Populus tremuloides	.....	1.1
Shrub stratum		
Rhamnus alnifolia	2.2	1.1
Rhus vernix	2.3	....
Acer rubrum	+.1	+.1
Prunus cf. *nigra*	+.1	+.1
Vaccinium corymbosum	+.2	+.1
Field stratum		
Osmunda cinnamomea	3.3	2.3
O. regalis	+.2	+.2
Onoclea sensibilis	2.2	1.2
Symplocarpus foetidus	3.2	1.2
Maianthemum canadense	1.3	2.2
Coptis groenlandica	+.2	1.3
Acer rubrum	+.1	2.1
Parthenocissus quinquefolia	+.1	1.1
Dryopteris spinulosa	+.2	+.2

and *Daucus Carota*. The surface is partly covered by a moss, *Brachythecium* sp. The soil is primarily a sandy loam except in the low moist places which have a slightly higher humus content. In comparison with the other areas, the old field is dry.

Hardwood Swamp.—This habitat, characterized by a mature stand of hardwood trees (*Acer rubrum*, *Ulmus americana*, and *Betula lutea*), lies in a low wet area. Although the soil is moist throughout the year, the northeastern (slightly higher) portion is somewhat drier. The lower portion is almost completely inundated during the fall and spring, and during the winter months when not frozen. The higher region contains a few small pools of standing water during these times.

A shrub stratum of young trees, *Rhus vernix* and *Ilex verticillata*, is present in the wetter places. A field stratum which consists of *Osmunda cinnamomea*, *O. regalis*, *Dryopteris spinulosa*, *Onoclea sensibilis*, *Symplocarpus foetidus*, *Impatiens capensis*, *Rubus pubescens*, *Coptis groenlandica*, and *Maianthemum canadense* is also well developed here. Shrub and field strata are little developed in the drier region (Table I).

TABLE II.—Partial Braun-Blanquet relevés from the spruce — birch — larch swamp and the spruce burn. The numbers indicate abundance-cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Spruce area	Birch-larch area	Burn area
Tree stratum			
Picea mariana	4.1	.....	.....
Larix laricina	1.1	2.1	.....
Betula lutea	.....	4.1	.....
Shrub stratum			
Vaccinium corymbosum	2.2	2.2	1.3
Gaylussacia baccata	+.2	2.2	.....
Ilex verticillata	+.1	.....	.....
Larix laricina	.....	+.1	+.1
Picea mariana	.....	+.1	2.1
Acer rubrum	.....	1.1	.....
Field stratum			
Maianthemum canadense	+.1	2.2	.....
Symplocarpus foetidus	+.2	.....	.....
Sarracenia purpurea	+.2	.....	+.1
Carex disperma	+.3	.....	.....
Vaccinium corymbosum	.....	1.1	.....
Acer rubrum	.....	1.1	.....
Osmunda cinnamomea	.....	+.3	.....
Dryopteris spinulosa	.....	+.2	.....
Chamaedaphne calyculata	.....	.....	4.5
Vaccinium macrocarpon	.....	.....	2.1

The relatively level surface of the drier portion is covered with a thin layer of leaf mold. The wet region is characterized by an irregular surface with hummocks (built largely by growth of *Osmunda cinnamomea*) rising approximately .25 meters above the surface. The hummocks are not covered by water during the wet season. *Sphagnum* sp. and other mosses are common here but are much less abundant in the drier sites. The wet portion is also characterized by having much more debris (deadfall timber and brush) on the surface.

The upper soil layers of this habitat are composed mainly of humus with only a small amount of mineral matter. A fibrous mass of roots gives the soil a spongy character.

Bog Mat.—A typical *Sphagnum* bog mat, located on the northern side of Mud Lake. The water level is usually 10 to 15 centimeters below the surface (in some places where the *Sphagnum* is absent, it is at the surface). The very wet substrate is composed almost entirely of peat with very little mineral matter. There are four distinct plant communities on the bog mat: (1) *Typha-Chamaedaphne;* (2) *Chamaedaphne*; (3) *Larix-Rhus*; and (4) *Carex-Scirpus.*

Black Spruce-yellow Birch-larch Swamp.—The vegetation of this habitat consists of two distinct types; a *Betula-Larix* swamp which gradates into a *Picea mariana* swamp (Table II).

The *Betula-Larix* portion is characterized by an open stand of *Betula lutea* and *Larix laricina.* A dense shrub stratum of *Vaccinium corymbosum, B. lutea,* and *Acer rubrum* is present. There are many fallen trees. The surface is covered with a leaf mold consisting mainly of birch leaves and larch needles. On lower ground some *Sphagnum* occurs.

The *Picea mariana* swamp contains sparse shrub and field strata. The canopy occurs to within 1 to 3 meters of the ground. The bases of the trees are surrounded by small, low hummocks rising 15 to 20 centimeters above the surface. These hummocks are covered by a litter layer of spruce needles and are comparatively dry. The low depressions contain *Sphagnum* and are moist. They hold standing water during the wet seasons.

The ground surface of the spruce stand presents the typical physiognomy of spruce growing on a shallow soil. Frost heaving and wind action have combined to produce either complete or partial windthrows. Owing to their shallow, spreading root system, the trees have raised portions of the soil surface, leaving open cavities below that are usually filled with water.

Spruce Burn.—A site within the spruce stand that burned approximately 27 years ago. It is characterized by a cover of *Sphagnum* with a uniform stand of leather-leaf (*Chamaedaphne calyculata*) and a few scattered small black spruce trees (*Picea mariana*). The surface is irregular with hummocks of *Sphagnum* up to half a meter in height surrounding the bases of the leather-leaf clones. Below the *Sphagnum* is a humus substrate containing some mineral matter and

charcoal, a remnant of the forest fire. The water table is .25 to .50 meters below the surface (depending upon the season). While the *Sphagnum* is relatively moist throughout the year, it is not so moist as that occurring in the bog. The hummocks in particular are relatively dry.

Oak-hickory Upland.—This habitat is located on an elevated glacio-fluvial deposit lying in a low marshy area. Its highest point is 4 to 5 meters above the surrounding marsh. It is covered by a mature oak-hickory stand. The dominant trees are *Carya ovata, Quercus alba,* and *Q. rubra.* A shrub stratum of young individuals of the dominant species, as well as *Pyrus coronaria, Prunus serotina,* and *Corylus americana* is of sporatic occurrence. Field stratum plants are common. The more abundant species are *Carex rosea, Aster macrophyllus, Galium boreale, Geranium maculatum, Pteridium aquilinum* var. *latiusculum, Rosa virginiana, Quercus alba,* and *Anemonella thalictroides* (Table III). A leaf mold is well developed over most of the site although it is partially obscured by sedges (*C. rosea*) in the localities free of shrubs. Numerous fallen trees and decaying stumps occur throughout. The soil is dry in comparison with that of the hardwood swamp.

The physiognomy of the vegetation closely resembles the drier portion of the hardwood swamp. There is considerable difference, how-

TABLE III.—Partial Braun-Blanquet relevés from the oak-hickory. A, from a portion with underbrush; B, from a portion with little underbrush. The numbers indicate abundance cover and sociability estimates in that order (for scales see Dansereau, 1957).

Species	Relevé A	Relevé B
Tree stratum		
Carya ovata	4.1	1.1
Quercus rubra	4.1	.....
Q. alba	2.1	5.1
Shrub stratum		
Corylus americana	2.3	.....
Prunus serotina	2.1	+.1
Field stratum		
Carex cf. *rosea*	2.2	4.3
Aster macrophyllus	3.3	2.3
Galium boreale	2.3	2.3
Geranium maculatum	2.1	2.1
Pteridium aguilinum	2.2	.....
Rosa virginiana	2.2	+.1
Corylus americana	2.1	.....
Quercus alba	2.1	.....
Anemonella thalictroides	1.1	1.1

ever, between that of the oak-hickory stand and wetter sites of the hardwood swamp.

Marsh.—The dominant plants in this habitat are sedges and grasses; one area contains primarily *Potentilla fruticosa* and another, a stand of *Solidago* sp. and *Aster* sp. There is considerable variation in species composition within the grass-sedge portion.

In general, the surface is low with the water table only a few centimeters below the surface. During the wet season, water stands over most of the area. Only the portions that support the *Solidago, Aster,* and *P. fruticosa* stands were not inundated during the study. Of these the *P. fruticosa* stand grows on the higher ground (.25 to 1.0 meter above the general level of the marsh surface). The soil throughout is typical of marshes (Dansereau, 1957); it contains much fibrous, peaty humus and a moderate amount of mineral matter. As indicated above, the soil moisture is high even when not inundated, being nearly saturated during the driest months. The sedges and grasses grow from small hummocks 5 to 10 centimeters in diameter and height. The spaces between the hummocks are usually free of living vegetation. In the slightly drier portions these hummocks may not be completely submerged during the wet season.

During the winter the dead vegetation falls over and forms a low canopy. Decaying vegetation also falls in between the hummocks to form a tangled mat that covers the surface. In the summer the grasses and sedges completely cover the surface.

Descriptions of the Transects.—Six transects were established to cross as many different habitats as possible. These transects were subdivided into different "segments" according to physiognomy of the vegetation, type of and moisture content of the substrate, leaf litter, and debris (logs, dead brush, and litter). A brief description of each of the 15 segments so established follows:

1. Moist, open swamp hardwoods.—Tree stratum well-developed (*Prunus virginiana, Betula lutea, Quercus macrocarpa,* and *Populus tremuloides*), canopy open; shrub stratum dense (*Rhus vernix, Vitis* sp., *Ilex verticillata, Acer rubrum,* and *P. tremuloides*); field stratum dense (*Impatiens capensis, Rubus pubescens, Vitis* sp., *Thalictrum dasycarpum, Aralia nudicaulis,* and *Onoclea sensibilis*); few mosses present; substrate primarily organic with some mineral matter present; moist; leaf mold thick; much debris on the surface (43% coverage). Length, 93 meters.
2. Wet, closed, swamp hardwoods.—Dense tree stratum (*Betula lutea, Acer rubrum,* and *Ulmus americana*), canopy closed; shrub stratum dense (*Rhus vernix, Ilex verticillata, A. rubrum,* and *B. lutea*); field stratum dense (*Osmunda cinnamomea, Onoclea sensibilis, Symplocarpus foetidus, Maianthemum canadense,* and *Rubus pubescens*); surface open between the clones of ferns; mosses abundant; substrate primarily organic with some mineral matter present, spongy; wet; leaf mold thin; much debris on the surface (28% coverage). Length, 312 meters.
3. Moist, closed, swamp hardwoods.—Tree stratum dense (*Acer rubrum* and *Ulmus americana*), canopy closed; sparse shrub and field strata;

few mosses present; substrate primarily organic with some mineral matter present; moist; leaf mold thick; little debris on the surface (16% coverage). Length 156 meters.

4. Sedge-fern bog.—Tree stratum absent; shrub stratum sparse (*Rhus vernix* and *Larix laricina*); field stratum dense (*Typha latifolia, Scirpus acutus, Carex lasiocarpa,* and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum,* little mineral matter present; wet; little debris on the surface (less than 1% coverage). Length, 120 meters.
5. Larch bog.—Low tree stratum present (*Larix laricina*), canopy closed; shrub stratum dense (*L. laricina, Betula lutea, Rhus vernix,* and *Cornus stolonifera*); field stratum present (*Osmunda cinnamomea, O. regalis,* and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum,* some mineral matter present; wet; some debris on the surface (less than 1% coverage). Length, 42 meters.
6. Leather-leaf bog.—Tree stratum absent; very low shrub stratum present (*Chamaedaphne calyculata* and *Vaccinium macrocarpon*); sparse field stratum; substrate peat, covered with *Sphagnum,* little mineral matter present; wet; no debris present. Length, 132 meters.
7. Cattail-leather-leaf bog.—Tree stratum absent; low shrub stratum present (*Chamaedaphne calyculata* and *Salix* sp.); field stratum dense (*Typha latifolia* and *Dryopteris Thelypteris*); substrate peat, covered with *Sphagnum,* some mineral matter present; very wet; some debris on the surface (less than 1% coverage). Length, 54 meters.
8. Birch-larch swamp.—Tree stratum well-developed (*Larix laricina* and *Betula lutea*), canopy open; shrub stratum dense (*Vaccinium corymbosum, Acer rubrum, B. lutea,* and *Gaylussacia baccata*); field stratum present (*A. rubrum* and *Maianthemum canadense*); some mosses present; substrate *Sphagnum* and decaying organic material, some mineral matter present; moist; leaf mold on dry places; much debris on the surface (50% coverage). Length, 96 meters.
9. Larch-spruce swamp.—Tree stratum very dense (*Larix laricina* and *Picea mariana*), canopy closed; shrub and field strata sparse; substrate organic with mineral matter present around the bases of the trees; wet; leaf mold thin; little debris on the surface (11% coverage). Length, 48 meters.
10. Spruce burn.—Tree stratum absent; shrub stratum dense (*Picea mariana, Chamaedaphne calyculata,* and *Vaccinium corymbosum*); field stratum sparse; substrate organic with little mineral matter present and covered with *Sphagnum;* moist; no leaf mold present; little debris on surface (2% coverage). Length, 108 meters.
11. Birch-poplar-maple swamp.—A few scattered trees (*Populus tremuloides, Acer rubrum,* and *Betula lutea*); shrub stratum dense (same species as tree stratum); field stratum present (*Maianthemum canadense, Onoclea sensibilis,* and sedges); some mosses present; much debris on the surface (38% coverage). Length, 120 meters.
12. Oak-hickory upland.—Tree stratum dense (*Quercus alba, Q. rubra,* and *Carya ovata*), canopy closed; shrub stratum present (*Prunus serotina, Pyrus coronaria, Corylus americana,* and *Cornus racemosa*); field stratum present (*Galium boreale, Aster macrophyllus, Carex rosea,* and *Anemonella thalictroides*); substrate mainly mineral matter, some organic material present; dry; leaf mold well developed; little debris on the surface (15% coverage). Length, 144 meters.
13. Composite marsh.—Tree and shrub strata absent; field stratum dense; forbs abundant (*Solidago* sp., *Aster* sp., and *Eupatorium purpureum,*

some grasses and sedges present; substrate decaying organic material, some mineral matter present; wet; much debris on the surface (100% coverage). Length, 96 meters.

14. Grass-sedge marsh.—Tree and shrub strata absent; field stratum dense, primarily of grasses and sedges; substrate organic with some mineral matter present; wet; much debris on the surface (100% coverage). Length, 72 meters.
15. *Potentilla* marsh.—Tree and shrub strata absent; field stratum present, primarily *Potentilla fruticosa*, some grasses and sedges present; substrate organic, some mineral matter present; moist; much debris on surface (100% coverage). Length, 87 meters.

METHODS

Most of the methods have been described elsewhere (Getz, 1959 and in press). Only those methods pertaining directly to the shrews are given in detail here; the remainder are summarized. The period of the study was September, 1957, through September, 1958.

Generalized Study.—A rectangular study area was established in each of the seven habitats described above. Each study area, except that in the burn area, contained 75 trap stations placed in a grid pattern with a 12 meter interval. The burn area was small and contained only 30 stations. All areas except the old field and marsh were snap-trapped for two, three-night periods (one trap at each station). The live-trapping data (see below) were utilized to get comparable data from the marsh and old field. The areas were trapped once in the fall (October and November, 1957) and again in the winter (January, 1958).

Study of the Marsh and Old Field.—The entire old field (2.5 hectares) and a 4.4-hectare portion of the marsh were marked off in a grid pattern with a 12-meter interval. Both areas were live-trapped for five nights each month from Setember, 1957, through September, 1958. Because of the large number of stations in the marsh, two trapping periods were required to cover all the stations. Live-traps of the type described by Burt (1940) were utilized. The traps were checked twice a day, once at 0800 to 1100 and again from 1600 to 1800 (for dates of trapping see Getz, 1959).

The live-traps were not efficient in capturing shrews. Most were able to escape by raising the trap-door. As a result relatively few captures were recorded (243 individuals caught a total of 405 times during the entire study). From the odor and feces in the trap, it could normally be determined when a shrew had entered a trap. Most of the data concerning the distribution of shrews were, therefore, obtained from signs rather than from actual captures.

Trap mortality was high for those individuals captured. Twenty-two per cent of the first captures of *B. brevicauda* were dead in the traps while 26 per cent of those alive at the first capture eventually were found dead in the traps. Of 74 individuals of *S. cinereus* taken, only nine were alive when first captured and two of these were eventually found dead in the traps. The *B. brevicauda* population was

undoubtedly reduced somewhat and almost the entire *S. cinereus* population was apparently removed for none was captured after April.

Transect Studies.—A trapping station was located every three meters along each transect. Each station was trapped (one snap-trap per station) for seven nights during the first two weeks of September, 1958. The capture data for each of the 15 segments were converted to a common factor (number of captures per 500 trap nights) for comparisons.

STUDIES OF ENVIRONMENTAL FACTORS

The techniques employed in the study of the environmental factors have been given in detail elsewhere (Getz, 1959). The factors studied included vegetation (type and physiognomy), cover, moisture (including standing water), temperature, and food.

Vegetation.—Line intercept transects were studied to determine vegetation types in all seven areas as well as along the trapping transects. Phytosociological studies were also made in all seven habitats. These data have been used to determine the types of vegetation present as well as the physiognomy.

Cover.—The amount of cover (percentage of coverage) in the form of logs, stumps, brush, leaf mold, and other debris, was determined from the line intercept data.

Moisture.—Substrate moistures were determined by gravimetric methods. Samples were taken from each habitat several times during the course of the study. These showed that all areas except the old field have practically saturated substrates at all times. The depth of standing water at each station in the marsh was recorded during each trapping period. The standing water in the swamps and bog were also indicated on the line intercept transects.

Temperature.—Temperatures were determined by stations located in each habitat. A station consisted of three max-min thermometers measuring temperatures one meter above the surface, 2.5 centimeters above the surface (leaf litter or snow when it was present), and 4.0 centimeters below the surface. Thermometers recording surface temperatures were placed at different sites within the marsh, old field, and hardwood swamp to obtain comparisons.

Food.—Information concerning the food habits of shrews is given by Hamilton (1930, 1941), Eadie (1944), Ingram (1942), and Shull (1907). From the food items listed in these papers, as well as from my own observations on captive specimens, it appears that a shrew will eat almost any small invertebrate it encounters. Since no evidence is at hand to contradict this, I have assumed all terrestrial invertebrates available to shrews to be potential sources of food. By comparing the amount of food items in the various habitats a rough estimate can be obtained of the relative availability of food.

To obtain estimates of the amount of potential shrew food available, several methods of sampling were employed. The basic method of sampling in all areas was one similar to that described by Shelford

(1929). An open-topped, one-twelfth square meter sampling ring was utilized. Representative portions of each study area were chosen and the ring tossed into the sites with the sample being taken where the ring came to rest. All the invertebrates on the surface or in the upper five centimeters of the substrate were recorded. Six such samples were taken at each site studied.

In the areas in which they occurred, logs were turned and a count made of all invertebrates found under them. Measurements were then made of the area covered by each log, and the number of logs in the habitat was estimated. In those areas being live-trapped the number of invertebrates that congregated in and under the traps was noted. Pitcher plants were also examined, and the numbers of invertebrates in them recorded. Finally, general observations were made to further add to these data.

In determining the comparative amounts of food available in the various areas, the data from the ring samples were used as a base. The data obtained from the other sampling methods were then evaluated to give a better indication for each habitat. The individual animals were not weighed, but each individual was assigned a "mass number" based on its size (indications of relative sizes of the individuals were recorded in the original notations). These were then totaled to give a comparative figure for each habitat.

Admittedly, these results are subjective. Numerous sources of error are present, one of which is the possible rejection of certain species by the shrews. Other factors such as seasonal and daily variations in activity patterns would tend to influence the apparent availability of food at any given time. The above sampling was done during May, 1958. Observations in all the habitats during the other months indicated that the relationships obtained in this study were not altered greatly.

STATISTICAL ANALYSIS

Those data that lend themselves to statistical treatment have been analyzed by use of the Chi-square test and the Spearman rank correlation coefficient (Siegel, 1956). In the following discussions the correlation coefficient (r_s) as well as the probability or level of significance (P), from Siegel (*op. cit.*), are given with statements of correlation or no correlation.

RESULTS

Blarina brevicauda

The shorttailed shrew is "most common in heavy forests and low, damp, swampy areas, but may be expected in practically every land habitat" (Burt, 1948). Other workers (Townsend, 1935; Pruitt, 1953; Enders, 1930; Dice and Sherman, 1922; Allen, 1938; and Wetzel, 1958) have demonstrated that *B. brevicauda*, occurs in most types of vegetation.

These same authors have also stated that *B. brevicauda* occurs in moist areas. Enders (*op. cit.*) further stated that it was more abun-

dant in well-drained (although moist) areas. Chew (1951) found that *B. brevicauda* had a high evaporation rate (twice that of *Peromyscus leucopus*). Furthermore it was unable to regulate evaporation in low humidities. This high evaporative loss indicates the necessity of a high humidity or a relatively high intake of free water to avoid desiccation. Pruitt (1959) found that *B. brevicauda* inhabited only those areas in which the soil moisture was high enough to saturate the air of its burrows. He concluded that a saturated air was required in the burrows of these animals in order for them to maintain a water balance. The food of *B. brevicauda* is composed of from 60 to 95 per cent water (Chew, *op. cit.*) This augments intake of free water.

Indications of a restriction to areas that have a well-developed leaf mold (Hanson, 1946; Pruitt, 1953) probably result from the indirect relationship of increased humidity under such a cover. In support of this, Jameson (1949) found that a leaf mold was not essential for the presence of *B. brevicauda*. Manville (1949) stated that "moisture seems to have somewhat less influence on the distribution of this species than on that of . . . *Sorex*."

Pearson (1947) found that *B. brevicauda* has a high metabolic rate (next to *S. cinereus* which had the highest rate of the 13 species tested). This indicates a need for an abundant supply of food. Hamilton (1930) has given data concerning the amount of food eaten by captive *B. brevicauda* that tend to confirm the voraciousness of this species. Eadie (1944) has shown *B. brevicauda* to feed extensively on *Microtus pennsylvanicus;* this relationship may influence its distribution.

Pruitt (1953, 1959) found that *B. brevicauda* avoids areas that display extreme temperature variations. However, I know of no studies concerning the temperature toleration of this mammal.

In the present study I attempted to investigate the influences of standing water, available food, and temperature upon this shrew. Information pertaining to vegetation, interspecific competition, and cover were also obtained. These are summarized under the appropriate headings.

Vegetation.—No response to the type of vegetation was indicated since *B. brevicauda* was present in most types ranging from grass-like to forested (Figs. 1 and 2). The high population densities in the

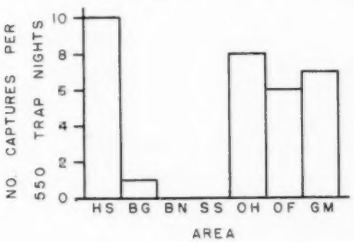

Fig. 1. — Relative abundance of *Blarina brevicauda* in the seven habitats of the generalized study. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, burn; SS, spruce-birch-larch swamp; OH, oak-hickory; OF, old field; GM, grass-sedge marsh.

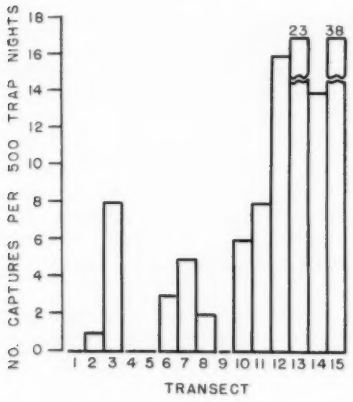

Fig. 2.—Transect captures of *Blarina brevicauda*

P. fruticosa area of the marsh (Fig. 3) appear to be a response to moisture conditions and not to the woody vegetation present in this area. Likewise, their absence in certain other types can be attributed to different factors as discussed below.

Cover.—The transect data showed that no correlation existed between the amount of cover (in the form of logs, brush, debris, etc.) in the various wooded habitats and the captures of *B. brevicauda* (r_s) — .11; *P*, .05 = .714). This species was also abundant in habitats in which such cover was absent. Cover (as defined above), therefore, has no significant influence upon the local distribution of

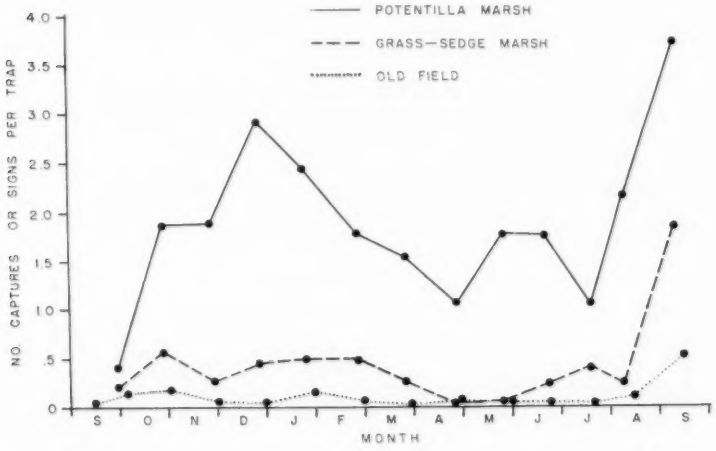

Fig. 3.—Captures and/or signs of *Blarina brevicauda* in the marsh and old field, September, 1957, through September, 1958

B. brevicauda. This appears particularly true in the birch-larch segment (No. 8) of the transects. This segment had a considerable amount of debris and logs on the surface and the soil was moist, but *B. brevicauda* was absent. Available food was low and appeared to be the limiting factor. Likewise, much cover was present in the hardwood swamp transect segments Nos. 1 and 2, but *B. brevicauda* was absent or quite scarce. No difference in number of captures occurred between segment No. 3 of the hardwood swamp, which had very little cover, and No. 11 of the birch-poplar-maple swamp, which had a great deal of cover. Leaf mold was not an important factor as *B. brevicauda* was abundant both where leaf mold was present and where it was absent (i.e., oak-hickory and marsh).

Moisture.—Avoidance of extremely dry areas was apparent from the live-trapping data of the old field (Fig. 3). Furthermore, most of the captures and signs were from the low, moist sites in the field.

Standing water was also avoided. Data from the marsh show very few captures or signs from stations that were inundated (Table IV). Furthermore, most of the inundated stations recording captures or signs were close to places where the surface was not covered with water. As soon as the standing water disappeared in the summer, *B. brevicauda* started moving into the portions formerly avoided. By September, 1958, the shorttailed shrew was distributed throughout most of the marsh.

The transect in the wetter portion of the hardwood swamp yielded few captures of *B. brevicauda*. Likewise no captures during the generalized study were obtained from the wetter portion of the study area. Water was present in this region during the fall, winter, and spring. Although it disappeared later in the summer, movement of *B. brevicauda* into the region may not have been rapid enough for the region to yield large numbers of captures. The fewer numbers on

TABLE IV.—Relation of captures and signs of *Blarina brevicauda* to depth of water. (Data represent compilations for all months standing water was present in the marsh.)

Average water depth[1]	No. of traps	No. of captures and signs	Average per trap
0	559	624	1.12
2.5	217	62	.28
5.0	100	5	.05
7.5	38	1	.03
10.0	63	2	.03
12.5	28	1	.04
15.0+	51	1	.02

[1] Depth of water measured in centimeters.

the bog may in part have resulted from excessive moisture, but food availability is probably a more important factor.

Food.—Since *B. brevicauda* is a rather large shrew, it tends to feed upon the larger species of invertebrates. The smaller food items (collembolans, ants, etc.) may be too small to furnish an adequate supply of food for *B. brevicauda.* This is in contrast to *S. cinereus,* which, owing to its small size, probably is more capable of capturing the smaller food items.

No correlation existed between the relative abundance of food in the various areas and the distribution of *B. brevicauda* (r_s, .15; *P*, .05 = .564). Similarly, no area had high population densities of *B. brevicauda* solely because of a greater availability of food (Fig. 4). This was particularly obvious in the higher parts of the old field during the summer. During this time, food availability was very high owing to the presence of numerous crickets, grasshoppers, and other insects. *B. brevicauda* almost completely avoided the area, however. A similar situation existed in the marsh. In the portion that contained standing water, food was more abundant than in the drier parts (e.g., *P. fruticosa* area). *B. brevicauda* avoided the former, however. Similarly, food was much less abundant in the drier parts of the hardwood swamp than in the wetter places, but *B. brevicauda* was much more abundant in the former.

Low amounts of available food appeared to have a definite influence on the local distribution of *B. brevicauda.* The burn and spruce-birch-larch swamp appeared to have favorable amounts of moisture and cover, but were deficient in available food. *B. brevicauda* was almost entirely absent from these two areas. Most of the individuals that were captured in the burn area were from near the edge of a birch-poplar stand that had a greater supply of food. The low food availability on the bog mat is probably the main factor responsible for the low numbers of *B. brevicauda* in this area.

Temperature.—Except in areas with little vegetation (i.e., the

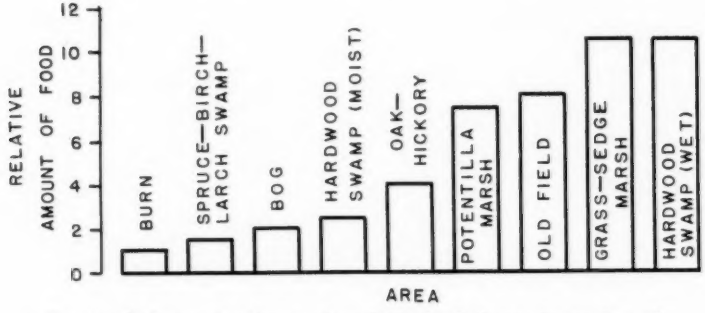

Fig. 4.—Relative abundance of available food (larger invertebrates) for shrews. Based on the burn area as one

parts of the old field in which the growth of grass was sparse) temperature probably did not exert a significant influence upon the local distribution of *B. brevicauda*. In some areas the stratum occupied by the shrews had extremely low temperatures. One such area was the hardwood swamp (Fig. 5); this area was inhabited by *B. brevicauda* during the winter. Observations of tracks and signs made during one of the coldest nights of the year, 4 January 1958 (surface temperature low of −20° C), showed that *B. brevicauda* had been active in all areas in which this species occurred. In most areas studied a sufficient amount of vegetation occurred for the animals to obtain shelter during periods of extremely low temperatures should they desire to do so. Areas such as the marsh (grass-sedge type), bog mat, and burn had relatively moderate temperatures (Getz, in press), but were not utilized extensively by *B. brevicauda*.

Few captures were obtained in the higher parts of the old field during the winter. As vegetation was sparse here and no other cover

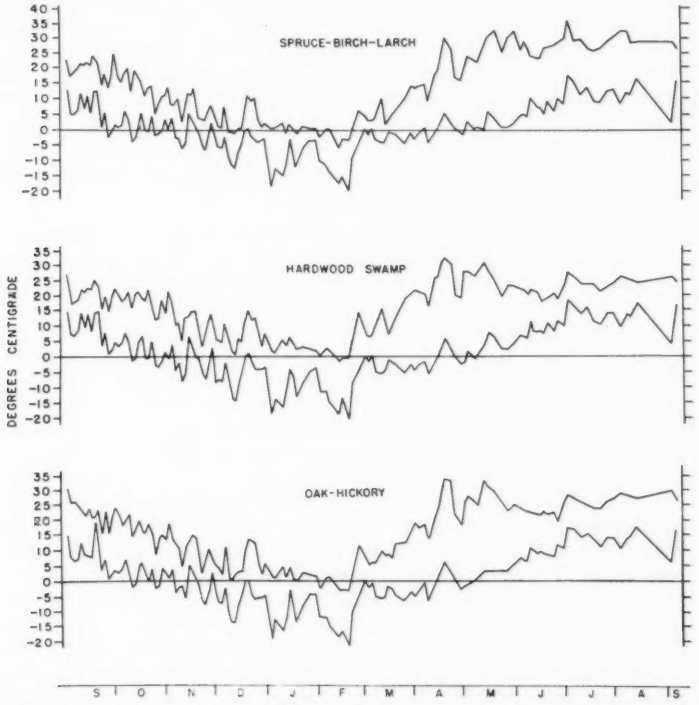

Fig. 5.—Maximum and minimum temperatures 2.5 cm above the surface. Thermometers were checked every two to four days, September, 1957, through September, 1958.

was available, temperatures undoubtedly were quite low. Only under such circumstances of very sparse cover does it seem probable that low temperatures influence local distribution of *B. brevicauda.* Similarly, high temperatures did not appear to exert any significant influence except perhaps in the old field. In all other areas at the level occupied by *B. brevicauda,* the temperatures apparently were moderated enough by the vegetation to prevent their being an important factor.

Interspecific Competition.—No obvious positive or negative influences of other species occurred. *B. brevicauda* was abundant in some areas in which *Sorex cinereus* was also abundant. In those areas in which *S. cinereus* was abundant, but in which *B. brevicauda* was absent or scarce, factors other than competition are more important. In the bog, spruce-birch-larch swamp and burn, the low available food supply appears to be responsible, while in the grass-sedge marsh (when it was inundated) standing water brought about an avoidance of the area on the part of *B. brevicauda.*

Predation Upon Voles.—Population densities were not higher in areas in which *Microtus pennsylvanicus* was abundant. Furthermore, *B. brevicauda* was often more abundant where *M. pennsylvanicus* did not occur (i.e., *P. fruticosa* area of the marsh). *B. brevicauda* was also abundant, however, in places in the marsh and old field in which *M. pennsylvanicus* was abundant. *M. pennsylvanicus,* therefore, did not appear to influence its distribution.

Conclusions.—*B. brevicauda* is not limited in its local distribution by any particular type of vegetation. It is found in all types ranging from entirely herbaceous to entirely woody. Areas with soil moisture lower than that required to keep the air in the burrows or in the humus saturated are not inhabited. Likewise, those areas in which the surface is inundated are avoided. Since *B. brevicauda* is unable to regulate evaporative losses to any extent, a relatively high humidity is required to reduce water losses when the animals are active. Any type of cover that allows the air to maintain a high humidity condition may be utilized. This can take the form of dense grass-like vegetation or a well-developed leaf mold.

Since *B. brevicauda* has a high rate of metabolism it requires a large intake of food. Areas in which the available food supply is low may be avoided regardless of the presence of other favorable conditions. This was demonstrated in the present work by the absence of *B. brevicauda* from the birch-larch swamp. This area appeared to have favorable conditions for *B. brevicauda* in all factors except food, the number of larger forms of invertebrates was very low. However, the presence of an abundant food supply is not the sole factor favoring the presence of the shorttail shrew. The old field (during the summer) and the inundated portion of the marsh both had greater amounts of available food than did other areas in which *B. brevicauda* was abundant. This species was very scarce in these situations, however. Unless other

factors are favorable, an abundant food supply thus has little apparent influence upon the local distribution of *B. brevicauda.*

The only obvious influence of cover is in areas in which the vegetation is extremely sparse. These areas are avoided during times of the year when temperature extremes are at a maximum. Sparse vegetation also results in low humidity conditions. Thus cover, humidity, and temperature are interacting factors. There seems to be little difference in abundance of *B. brevicauda* when one compares areas that differ in the number of fallen trees, stumps, and debris present. Within a given habitat, population densities may be somewhat higher where cover is more abundant owing to increased availability of homesites or shelter from temperature extremes, but this was not demonstrated in the present study.

Temperature apparently becomes a factor in local distribution only in those areas in which vegetation is sparse (e.g., denuded or with sparse herbaceous vegetation). The differences in temperature in other areas are not normally great enough to have any appreciable influence upon the local distribution of *B. brevicauda.*

The influence of other species upon the local distribution of *B. brevicauda* did not appear to be of major importance. Whenever such a relationship appeared possible, other factors were seen as more probable.

Sorex cinereus

The masked shrew occurs in a wide variety of situations within its range (Burt, 1948). It apparently prefers no particular type of vegetation since it is found in forested and grassy areas as well as in various intermediate types. Although not found in upland hardwoods in southern Michigan, *S. cinereus* occurs in this type of vegetation in northern Michigan (Burt, personal communication). Therefore, a negative response to such a vegetation type is not to be expected.

That moisture is a factor in its local distribution has been shown by Manville (1949), Pruitt (1953), and Townsend (1935). Manville (*op. cit.*) indicated that *S. cinereus* was more dependent upon a moist environment than was *Blarina brevicauda.* Cahn (1937) found that *S. cinereus* apparently avoided wet swamps in Ontario although it was abundant in areas bordering the swamps. As with *B. brevicauda,* the food of *S. cinereus* has a water content of 60 to 95 per cent which augments intake of free water.

Pearson (1947) found that *S. cinereus* had the highest rate of metabolism of any of the 13 species of small mammals he tested (including *B. brevicauda*). This necessitates a high intake of food in order to supply an ample source of energy if the animals are to maintain themselves.

The present study was primarily an attempt to determine the influence of moisture, temperature, and food upon the distribution of *S. cinereus.* It was also desired to obtain comparisons between the responses of this species and *B. brevicauda.*

Vegetation.—*S. cinereus* occurred in all general types of vegetation except the oak-hickory upland (Figs. 6 and 7). There was no significant difference in the distribution between the other areas. They were found in the drier portion of the hardwood swamp which is similar in physiognomy to the oak-hickory habitat. Thus, no selection or avoidance of woody or herbaceous plants nor physiognomy of the vegetation was apparent.

Cover.—There was no correlation between the amount of cover present in the woody areas (logs, brush, etc.) and the captures of *S. cinereus* (r_s, .47; *P*, .05 = .714). They were also abundant in areas entirely lacking such cover. Cover of this type, therefore, does not appear to be an important factor in the distribution of *S. cinereus*. They were also found in areas not having a leaf mold as well as in those where it was present.

Moisture.—*S. cinereus* occurred in areas with all degrees of moisture, except dry portions of the old field. Data from the marsh (during the months when it was partly inundated) showed that *S. cinereus* was most abundant where standing water was present (Fig. 8). The masked shrew thus differed markedly from the shorttailed shrew in this aspect. When no standing water was present *S. cinereus* was found in the areas that had previously had standing water. As has been noted, trap mortality of *S. cinereus* was high and most were killed by the trapping. The population was thus disturbed to a point where the summer data from the marsh are meager.

Food.—No correlation existed between the availability of the larger invertebrates and the distribution of *S. cinereus*. This species is probably able to utilize small food items such as ants, collembolans, and other small invertebrates. These forms are present in sufficient numbers in most areas to furnish an ample supply of food. Abundance of food likewise did not result in a larger population in any particular area. The *P. fruticosa* area of the marsh and the entire old field both had a considerable amount of available food (Fig. 4). These two areas were avoided by *S. cinereus*. Likewise, the oak-hickory, which was also avoided, had a greater available food supply than did several of the other areas in which *S. cinereus* was abundant.

Temperature.—As with *B. brevicauda*, temperature did not appear to play a significant role in the local distribution of *S. cinereus*. In

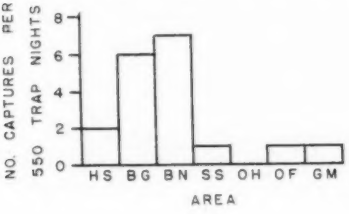

Fig. 6.—Relative abundance of *Sorex cinereus* in the seven habitats of the generalized study. Fall and winter trapping data combined. HS, hardwood swamp; BG, bog mat; BN, burn; SS, spruce-birch-larch swamp; OH, oak-hickory; OF, old field; GM, grass-sedge marsh.

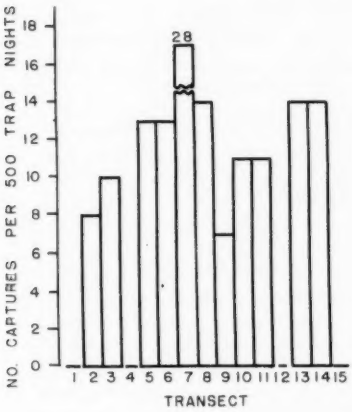

Fig. 7.—Transect captures of *Sorex cinereus*

areas in which a leaf mold or *Sphagnum* was present, the shrews were primarily active below the surface. Where such a cover was not present, as in the marsh, grasses or sedges normally covered the surface. In such areas where the shrews were active under the cover of vegetation or a leaf mold, the temperatures they encountered were relatively moderate (Fig. 5; Getz, in press). Although some activity may have occurred on the surface, *S. cinereus* was abundant in situations having the most extreme surface temperatures (i.e., bog mat and spruce burn). A further indication that low temperatures did not influence the distribution of *S. cinereus* was found in the spruce swamp. There was little cover in the form of a leaf mold in this habitat and the shrews were primarily active on the surface. Although temperatures were at times quite low on the surface, *S. cinereus* was abundant here. That relatively few individuals were captured in the old field is most likely a result of the combined effects of low humidity and temperature extremes.

Interspecific Competition.—No major influence upon the distribution of *S. cinereus* by other species was apparent. The absence of *S. cinereus* in the *P. fruticosa* area of the marsh and in the oak-

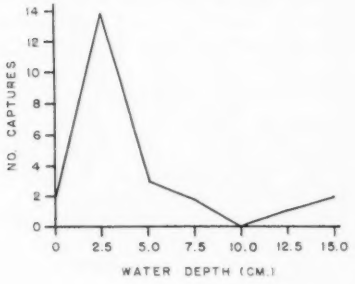

Fig. 8.—Relationship of captures of *Sorex cinereus* and depth of standing water in the marsh. Total captures during months standing water was present, October, 1957, through May, 1958.

hickory may have been in part a result of the high population densities of *B. brevicauda* in these areas. Both species were abundant in other areas, however, so that competition does not appear to be a primary factor involved in the local distribution of *S. cinereus*.

Conclusions.—The type or physiognomy of the vegetation has no apparent influence upon the local distribution of *S. cinereus*. In the more southern parts of its range it avoids upland hardwoods, but since this type of vegetation is inhabitated in the more northern regions, factors other than the type of vegetation are probably involved.

As in the case of *B. brevicauda*, *S. cinereus* is restricted to moist situations. It was comparatively less abundant in the old field than was *B. brevicauda*, suggesting less tolerance to low humidity. In contrast to *B. brevicauda*, it is present in areas in which the surface is inundated.

S. cinereus is small and is able to utilize smaller food items than is *B. brevicauda*. Since the small invertebrates are quite abundant in almost all areas, food is not an important factor in the local distribution of *S. cinereus*.

Temperature differences had no obvious influence upon the local distribution of *S. cinereus* except in those areas in which the vegetation was very sparse. Such a situation, an old field, was present in this study, but it was also quite dry and this may have been a factor in its avoidance by *S. cinereus*.

In certain situations high population densities of *B. brevicauda* may result in fewer numbers or in the absence of *S. cinereus*. This does not appear to be a general factor, however, as both species occur in abundance in other situations.

DISCUSSION

The most important factor influencing the local distribution of *Sorex cinereus* and *Blarina brevicauda* is moisture. As has been found by Pruitt (1953, 1959), these species probably can permanently inhabit only those situations in which the air humidities approach saturation. *B. brevicauda* did not occur where standing water was present; *S. cinereus*, on the other hand, was abundant under such conditions. The difference in response to standing water could not be explained in the present study. *S. cinereus* is a more agile animal than is *B. brevicauda* (based on observations of the two species in captivity). This greater agility combined with a lesser body weight and longer tail, which facilitates balancing, may allow *S. cinereus* to run above the surface of the water on the leaves of the grasses and sedges. *B. brevicauda* is of more stocky build and less agile so that it probably cannot maneuver on the vegetation so easily.

Within situations having favorable moisture conditions, food appears to be the most important factor influencing the distribution of *B. brevicauda*. This species is absent from those areas having rela-

tively low food availability (in the form of larger invertebrates: beetles, snails, earthworms, etc.). *S. cinereus* was not so influenced by fewer numbers of such food items. Although the larger invertebrates were scarce in some habitats, the smaller forms (ants, collembolans, and spiders) were abundant in all. It is possible, therefore, that *S. cinereus*, owing to its smaller size (especially its small teeth), may be able to utilize smaller food items than can *B. brevicauda*. As a result there would be an adequate food supply in almost all situations.

The primary importance of cover appears to be its influence upon humidity. The main requirement is the presence of cover to maintain high humidity conditions, whether it be in the form of a leaf mold, moss, or vegetation (particularly graminoids). In areas where cover is sparse, humidity conditions may be unfavorable for part of the day during certain times of the year. Although some species of small mammals may alter their activity patterns so as to avoid short periods of unfavorable conditions (Getz, in press), this may not be possible for shrews. Owing to their high metabolic rates and the resulting necessity for large intakes of food, shrews probably have to remain active throughout the day and night to obtain sufficient quantities of food. As a result they could not permanently inhabit situations in which the humidity conditions become unfavorable for extended periods.

REFERENCES

ALLEN, D. L. 1938. Ecological studies on the vertebrate fauna of a 500-acre farm in Kalamazoo County, Michigan. *Ecol. Monogr.*, **8**:347-436.

BURT, W. H. 1940. Territorial behavior and populations of some small mammals in southern Michigan. *Misc. Publ. Mus. Zool. Univ. Mich.*, **45**: 1-58.

———1948. *The Mammals of Michigan*. Univ. Mich. Press, Ann Arbor, 288 pp.

CAHN, A. R. 1937. Mammals of Quetico Provincial Park of Ontario. *J. Mamm.*, **18**:19-30.

CHEW, R. W. 1951. The water exchanges of some small mammals. *Ecol. Monogr.*, **21**:215-225.

DANSEREAU, P. 1957. *Biogeography. An ecological perspective*. Ronald Press, New York, 394 pp.

DICE, L. R. AND H. B. SHERMAN 1922. Notes on the mammals of Gogebic and Ontonagon Counties, Michigan, 1920. *Occ. Pap. Mus. Zool. Univ. Mich.*, **109**:1-46.

EADIE, W. R. 1944. The shorttailed shrew and field mouse predation. *J. Mamm.*, **25**:359-364.

ENDERS, R. K. 1930. Some factors influencing the distribution of mammals in Ohio. *Occ. Pap. Mus. Zool. Univ. Mich.*, **212**:1-27.

FERNALD, M. L. 1950. *Gray's Manual of Botany*. Eighth (centennial) edition. American Book Co., New York, 1632 pp.

GETZ, L. L. 1959. An analysis of some of the factors influencing the local distribution of small mammals in southern Michigan. Ph.D. thesis. Univ. Mich. 186 pp. Univ. Microfilms. Ann Arbor, Mich.

———In press. Factors influencing the local distribution of *Microtus* and *Synaptomys*. *Ecology*.

HAMILTON, W. J. 1930. The food of Soricidae. *J. Mamm.*, **11**:26-39.

———1941. The food of small forest mammals in eastern United States. *Ibid.*, **22**:250-263.

HANSON, H. C. 1946. Small mammal censuses near Prairie du Sac, Wisconsin. *Trans. Wisc. Acad. Sci., Arts and Letters*, **36**:105-129.

INGRAM, W. M. 1942. Snail associates of *Blarina brevicauda talpoides* (Say). *J. Mamm.*, **23**:255-258.

JAMESON, E. W. 1949. Some factors influencing the local distribution and abundance of woodland small mammals in central New York. *Ibid.*, **30**:221-235.

MANVILLE, R. H. 1949. A study of small mammal populations in northern Michigan. *Misc. Publ. Mus. Zool. Univ. Mich.*, **73**:1-83.

PEARSON, O. P. 1947. The rate of metabolism of some small mammals. *Ecology*, **28**:127-145.

PRUITT, W. O. 1953. An analysis of some physical factors affecting the local distribution of the shorttail shrew (*Blarina brevicauda*) in the northern part of the Lower Peninsula of Michigan. *Misc. Publ. Mus. Zool. Univ. Mich.*, **79**:1-39.

———1959. Microclimates and local distribution of small mammals on the George Reserve, Michigan. *Ibid.*, **109**:1-27.

SHELFORD, V. E. 1929. *Laboratory and Field Ecology*. Williams and Wilkins, Baltimore. 608 pp.

SHULL, A. F. 1907. Habits of the shorttailed shrew, *Blarina brevicauda* (Say). *Amer. Nat.*, **41**:495-522.

SIEGEL, S. 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Co., New York. 312 pp.

TOWNSEND, M. T. 1935. Studies on some of the small mammals of central New York. *Roosevelt Wildlife Annals*, **4**:1-120.

WETZEL, R. M. 1958. Mammalian succession on midwestern flood plains. *Ecology*, **39**:262-271.

Studies of the Byron Bog in Southwestern Ontario. XII. A Study of the Population of Insects Emerging as Adults from Redmond's Pond in 1957[1]

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ABSTRACT: Between March 23 and October 4, 1957, 13,159 adult insects were trapped in five tent-traps set out on the pond on water up to 3 ft. deep. The orders represented were Ephemeroptera (0.02%), Odonata (0.12%), Trichoptera (0.3%), Hemiptera (0.02%), Coleoptera (0.04%) and Diptera (99.5%). Midges of the family Chironomidae constituted 78.3% of the Diptera and Culicidae 21% of the Diptera. Other families of Diptera were Tipulidae, Ceratopogonidae, Dolichopodidae, Simuliidae, Tabanidae, Ephydridae and Muscidae. Families of Coleoptera were Helodidae and Chrysomelidae. The numbers and seasonal occurrences, including times of maximum emergence, are reported for each species.

In 1956 a collection of insects emerging from Redmond's Pond in the Byron Bog was made by trapping the insects in a floating tent-trap (Judd, 1958b). In 1957 a second study of the aquatic insects of Redmond's Pond was undertaken using five tent-traps set out on the pond. The present paper is a report on this study.

Acknowledgment.—The writer gratefully acknowledges the assistance of Mr. R. B. Catalan who aided throughout the summer of 1957 in collecting insects from the traps, in sorting and counting specimens and in recording data. Much of the data were assembled while the writer held a Summer Research Associateship of the National Research Council in 1957.

Description of Collection Sites

Redmond's Pond is situated in the northwest corner of the Byron Bog as shown on the map accompanying the description of the bog (Judd, 1957b). It is completely surrounded by the sphagnum mat which forms the center of the bog, and the bushes of leatherleaf, *Chamaedaphne calyculata*, which grow in the sphagnum, have their branches extending out over the water of the pond. In 1957 the pond was 240 feet long in the north-south direction and 160 feet wide at its greatest diameter (Fig. 1). The water depth remained almost constant during the summer and nowhere on the pond was it more than five feet. The bottom of the pond was covered with loose, brown peat. No attempt was made to measure the depth of the peat in 1957, but Woolverton (1900) found that the peat in the center of the Byron Bog was at least 60 feet deep. The surface of the pond was devoid of vegetation in 1957 except in small bays around the circumference.

[1] Contribution from the Department of Zoology, University of Western Ontario; a project supported by funds from the Ontario Research Foundation and an operating grant from the National Research Council.

On March 14, 1957 the pond was still completely covered by ice and by March 16 all the ice had melted away. Thereafter light shell ice formed on the water at the edge of the pond on cooler nights during March. On March 23 traps 1, 3 and 5 were set in position at locations around the edge of the pond, and on March 30 traps 2 and 4 were set in position in the deeper water toward the center of the pond (Fig. 1). Location "6" on the map is the site at which the single trap was anchored in 1956. Each trap was kept in its one position during the season by a rope anchored at one end to bricks on the bottom of the pond and stapled at the other end to the side of the trap. The inside dimensions of each trap were 2 ft. x 2 ft. so the trap covered 4 sq. ft. of water surface. The traps were kept in position until October 4 when collections were discontinued. Thin shell ice formed at the edge of the pond on that day.

Trap 1 was located in a small bay in the north-east corner of the pond surrounded by bushes of leather leaf and on water 2 feet deep. Rooted vegetation in and around the trap comprised Spatterdock, *Nuphar advena* (Ait) Ait. f. and Bladderwort, *Utricularia vulgaris* L. Floating on the surface was a sparse accumulation of fronds of Duckweed, *Lemna minor* L. and Water Flax-seed, *Spirodela polyrhiza* (L.) Schleid. Trap 2 was located in the center of the pond on water 3 feet deep where there was no vegetation. Trap 3 was located at the west edge of the pond in water 2 feet deep where rooted plants of *Utricularia vulgaris* were present and a few fronds of *Lemna minor* and *Spirodela polyrhiza* floated at the surface. Trap 4 was toward the center of the pond on water 3 ft. deep

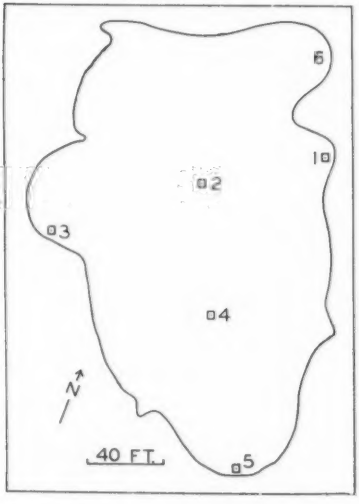

Fig. 1.—Map of Redmond's Pond showing location of the five tent-traps (1-5). Location "6" is the site of the trap on the pond in 1956.

where there was no vegetation. Trap 5 was at the south end of the pond over a floating shelf of moss extending from the edge of the pond. Thus the trap was floating in water 1 foot deep over a mat of sphagnum and other mosses and had in and around it a heavy growth of rooted plants of *Nuphar advena* and *Utricularia vulgaris*.

METHODS

Each day until October 4 the insects caught in each trap were collected. One side of the trap was raised above the surface of the water and an aspirator was passed into the trap and small insects were sucked up into it. Larger insects, such as dragon-flies, were picked from the lower surface of the screen with the fingers. The insects so collected were put into a killing jar and taken to the laboratory for sorting, counting, pinning (or preserving in fluid) and labelling.

The various groups of insects were identified by the following taxonomists, who, unless otherwise noted, are staff members of the Entomology Research Division, United States Department of Agriculture (USDA) or of the Entomology Research Institute, Canadian Department of Agriculture (CDA): C. P. Alexander, University of Massachusetts, Amherst (Tipulidae), W. J. Brown, CDA (Coleoptera), J. G. Chilcott, CDA (Ephydridae, Muscidae), D. M. Davies, McMaster University, Hamilton, Ontario, (Simuliidae), F. P. Ide, University of Toronto (Ephemeroptera), L. A. Kelton, CDA (Hemiptera), J. F. McAlpine, CDA (Tabanidae), A. Stone, USDA (Culicidae), J. R. Vockeroth, CDA (Dolichopodidae), E. M. Walker, Royal Ontario Museum, Toronto (Odonata), G. B. Wiggins, Royal Ontario Museum (Trichoptera), W. W. Wirth, USDA (Ceratopogonidae, Chironomidae).

All specimens are retained in the collections of the Department of Zoology, University of Western Ontario except as noted (USNM—United States National Museum, CNC—Canadian National Collection, ROM—Royal Ontario Museum) in the following account.

ACCOUNT OF TOTAL CATCH

The numbers of the insects in the six orders collected from the traps are presented in Table I. During the whole period that the traps were in operation, March 23 to October 4, 13,159 insects were trapped. Most of the insects are species whose larvae or nymphs live submerged and whose adults emerge from the water, but a few are insects that dwell on emergent aquatic vegetation. The great majority (99.5%) were Diptera and among these the Chironomidae predominated (78.3%). Next in point of numbers (21%) were the Culicidae. The other families of Diptera were present in much smaller numbers.

The most productive site was Trap 5, yielding more than half the total catch. It was in shallow water over a mat of moss and surrounded by aquatic vegetation. The least productive sites were

TABLE I.—Number of insects of the six orders collected in the traps

Group	Trap 1		Trap 2		Trap 3		Trap 4		Trap 5					
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	% of Diptera	No.	% of Total
Ephemeroptera	0	0	0	0	1	50	0	0	1	50			2	0.02
Odonata	0	0	0	0	1	7	1	7	13	86			15	0.12
Trichoptera	1	2	2	4	0	0	8	22	27	72			38	0.30
Hemiptera	0	0	0	0	2	100	0	0	0	0			2	0.02
Coleoptera	1	25	0	0	2	50	0	0	1	25			4	0.04
Diptera														
Tipulidae	1	100	0	0	0	0	0	0	0	0	1	0.01		
Chironomidae	1,012	10	1,007	10	647	7	519	5	7,068	68	10,253	78.30		
Ceratopogonidae	8	17	3	6	14	29	17	37	5	11	47	0.47		
Culicidae	394	14	296	11	916	33	183	7	986	35	2,775	21.00		
Dolichopodidae	0	0	0	0	0	0	0	0	2	100	2	0.02		
Simuliidae	5	72	1	14	0	0	0	0	1	14	7	0.07		
Tabanidae	0	0	0	0	0	0	1	100	0	0	1	0.01		
Ephydridae	0	0	0	0	0	0	0	0	11	100	11	0.11		
Muscidae	0	0	0	0	0	0	0	0	1	100	1	0.01		
Total Diptera	1,420	11	1,307	10	1,577	12	720	5	8,074	62	13,098	100.00	13,098	99.50
TOTALS	1,422	11	1,309	10	1,583	12	729	5	8,116	62			13,159	100.00

at Traps 2 and 4 where there was no vegetation. Traps 1 and 3, in which some vegetation was present, were more productive than Traps 2 and 4 but much less so than Trap 5. The area of water surface covered by each trap was 4 sq. ft., so the total area from which the insects were collected was five times this area, 20 sq. ft. Over the whole season 13,159 insects were trapped, an average yield of 658 insects per sq. ft. The average catch per sq. ft. for the five traps, respectively, was 356, 327, 396, 182, 2029 insects. The first insects emerged on April 21 and the last on October 4. The time of maximum emergence was the first week of June owing to large emergences of *Calopsectra* sp. and *Chaoborus flavicans* (Fig. 4).

The proportionate numbers of insects of the six orders trapped in 1957 (Table I) were closely similar to those caught in the single trap in 1956 (Judd, 1958b).

Account of Species Collected

The five bracketed numbers following the name of each species are the numbers of that species trapped, respectively, in the five traps.

EPHEMEROPTERA

BAETIDAE

Callibaetis sp.—2 mayflies (0 : 0 : 1 : 0 : 1); August 28.

ODONATA

COENAGRIIDAE

Enallagma ebrium (Hagen)—1♀ (0 : 0 : 0 : 0 : 1); June 10. This species was also trapped in shallow, weed-choked water in the Dundas Marsh (Judd, 1953), a habitat similar to that at Trap 5 where the specimen emerged in Redmond's Pond. Walker (1953) reports that sphagnum-bog ponds are unfavorable to this species.

Enallagma boreale Selys—2♂♂, 3♀♀ (0 : 0 : 1 : 0 : 4); May 24- June 7. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b). Its period of emergence in the bog is in accord with the estimate of Walker (1953) that its earliest recorded date of emergence is May 16 and that although it is sometimes very abundant in June, its numbers are already dwindling before the end of this month.

Enallagma hageni (Walsh)—1♀ (0 : 0 : 0 : 1 : 0); June 24. Walker (1953) notes that this species is tolerant of acid waters.

AESCHNIDAE

Anax junius (Drury)—1 dragon-fly (0 : 0 : 0 : 0 : 1); August 4. This species was trapped also on August 9 in 1954 at London (Judd, 1957a). Walker (1958) reports that its main period of emergence begins early in August.

LIBELLULIDAE

Sympetrum vicinum (Hagen)—2♂♂, 5♀♀ (0 : 0 : 0 : 0 : 7); July 26-August 18. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b). Its emergence from the shallow water at Trap 5 is in accord with the report by Judd (1953) that it emerged from shallow water in the Dundas Marsh.

TRICHOPTERA

LEPTOCERIDAE

Triaenodes nox Ross—2♂♂ (0 : 0 : 0 : 0 : 2) (ROM) June 27, August 14. Ross (1944) records this species from Ontario.

Triaenodes sp.—2♀♀ (0 : 0 : 0 : 0 : 2) (ROM); June 20, August 10.

Oecetis inconspicua (Walker)—14♂♂, 10♀♀ (1 : 0 : 0 : 1 : 22) (ROM); June 14-September 2, maximum July 30 (4 insects), Figure 2. This species was trapped also in 1956 both from Redmond's Pond (Judd, 1958b) and South Walker Pond (Judd, 1960) near London. The preponderance of this species in Trap 5 may possibly be explained by the fact that the larvae of *O. inconspicua* are predaceous (Ross, 1944) and would thus find abundant food in the large concentration of other insects at this site.

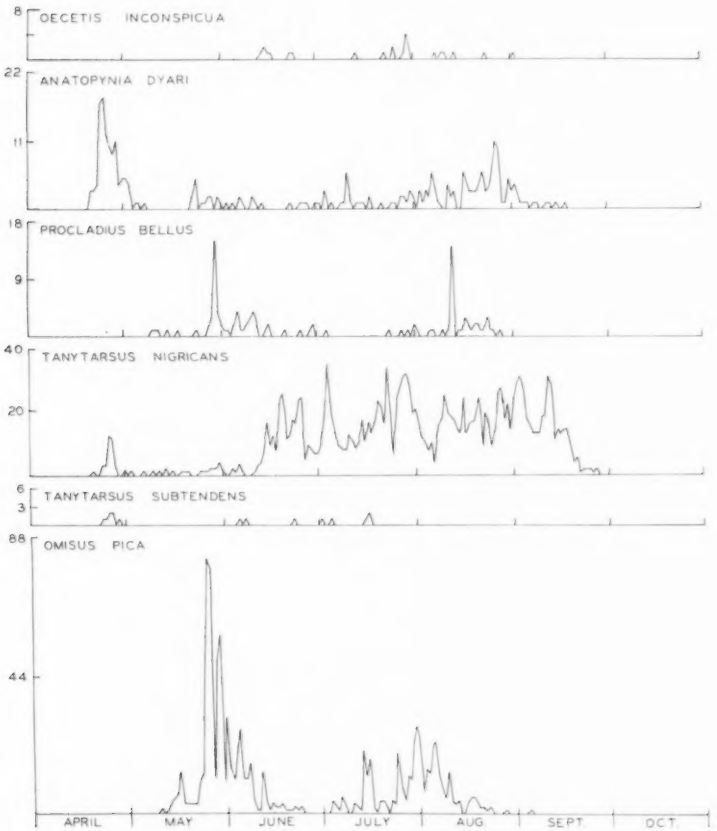

Fig. 2.—Periods of emergence of adult insects

PHRYGANEIDAE

Agrypnia vestita (Walker)—1 ♀ (0 : 0 : 0 : 0 :1) (ROM); June 4. Ross (1944) reports that this species occurs in lakes and marshes.

Banksiola crotchi (Banks)—7 ♀ ♀ (0 : 1 : 0 : 6 : 0) (ROM); June 20-July 9. This species emerged only in the open water at Traps 2 and 4. Ross (1944) records it from Canada in British Columbia.

HYDROPSYCHIDAE

Cheumatopsyche sp.—1 ♀ (0 : 0 : 0 : 1 : 0) (ROM); August 26.

HYDROPTILIDAE

Hydroptila perdita Morton—1 ♂ (0 : 1 : 0 : 0 : 0) (ROM); June 21. Ross (1944) gives records from Ontario and Judd (1957a) trapped this species at London.

HEMIPTERA

SALDIDAE

Saldula opacula (Zett.)—2 bugs (0 : 0 : 2 : 0 : 0); June 12, 18. The shore bugs are reported by Usinger *et al.* (1956) to inhabit situations including springs and bogs. *S. pallipes* was trapped on Redmond's Pond in 1956 by Judd (1958b).

COLEOPTERA

HELODIDAE

Scirtes tibialis Guérin—2 beetles (1 : 0 : 1 : 0 : 0); July 22, August 4. Usinger *et al.* (1956) refer to reports that the larva of this beetle feeds on duckweed and that the pupa forms on the same plant. Duckweed was found on Redmond's Pond in 1957 particularly at Traps 1 and 3 where the beetles were trapped. The time of emergence of the two beetles is in accord with the report of Kraatz (1918) that the adults become increasingly abundant up to the latter part of July, after which there is a rapid decline until the last week of August.

Cyphon variabilis Thunb.—1 beetle (0 : 0 : 1 : 0 : 0); June 5. Usinger *et al.* (1956) give records of larvae of *Cyphon* occurring in ponds and in wet moss and under stones around springs.

CHRYSOMELIDAE

Longitarsus sp.—1 beetle (0 : 0 : 0 : 0 : 1); April 21. Judd (1960) records trapping *Longitarsus* sp. on South Walker Pond in 1956.

DIPTERA

TIPULIDAE

Limnophila laricicola Alex.—1 cranefly (1 : 0 : 0 : 0 : 0); May 28. Alexander (1942) reports that this species is characteristic of sphagnum bogs and gives records of its occurrence in some of the northern United States.

CHIRONOMIDAE

Pentaneura monilis (L.)—4 ♂ ♂ (2 : 1 : 0 : 0 : 1); June 1, 28, July 12, August 8. This species was trapped in much larger numbers than in Redmond's Pond both on the Dundas Marsh (Judd, 1953) and on South Walker Pond (Judd, 1960).

Pentaneura spp.—1 ♂, 15 ♀ ♀ (4 : 1 : 5 : 0 : 6); May 14-August 4.

Pelopia stellata (Coq.)—5 ♂ ♂, 4 ♀ ♀ (0 : 0 : 0 : 2 : 7); June 10-July 8, August 21. This species was also trapped in 1956 in the water of the hypolimnion at South Walker Pond (Judd, 1960).

Clinotanypus thoracicus (Lw.)—1♀ (0 : 0 : 1 : 0 : 0); June 14. This species was also trapped in 1956 from South Walker Pond (Judd, 1960).

Anatopynia dyari (Coq.)—178♂♂, 109♀♀ (31 : 31 : 52 : 26 : 147); April 21-September 18, maxima April 25, August 27 (18, 11 insects), Figure 2. This species was also trapped from pools at London (Judd, 1957a), from South Walker Pond (Judd, 1960) and from Redmond's Pond (Judd, 1958b) when the times of emergence were in June.

Procladius culiciformis (L.)—6♀♀ (0 : 1 : 0 : 2 : 3); May 27-August 10. This species was trapped also in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

Procladius bellus (L.)—52♂♂, 55♀♀ (7 : 13 : 26 : 17 : 44); May 10-August 28, maxima May 30, August 13 (15, 14 insects), Figure 2. This species was trapped also in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960) being well-distributed through the season at all three locations.

Hydrobaenus sp.—1♀ (0 : 0 : 0 : 0 : 1); April 22.

Polypedilum sp.—3♂♂ (0 : 2 : 1 : 0 : 0); June 6, 21, July 11.

Tanytarsus nigricans (Joh.)—853♂♂, 849♀♀ (70 : 380 : 217 : 281 : 754); April 21-September 27, Figure 2. The emergence of this species remained high during the season after an upsurge in June. It was also trapped in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

Tanytarsus subtendens Townes—15♂♂ (8 : 0 : 0 : 7 : 0); April 24-July 17, Figure 2. This species was also trapped in 1956 from Redmond's Pond (Judd, 1958b).

Tanytarsus punctipes (Wied.)—258♀♀ (6 : 233 : 1 : 2 : 16); May 14-September 23, maximum August 31 (31 insects), Figure 3. Most of these midges emerged in the open water at Trap 2. The species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) where it also showed a maximum emergence at the end of August. It was found also at South Walker Pond in 1956 (Judd, 1960).

Omisus pica Townes—448♂♂, 499♀♀ (474 : 3 : 5 : 1 : 464); May 11-September 5, maxima May 26, July 31 (81, 28 insects), Figure 2. This species was also trapped in 1956 on Redmond's Pond (Judd, 1958b) when it also showed two peaks of emergence, one in spring and the other later in the summer. Its heavy emergence in Traps 1 and 5 indicates that the larvae dwell in shallow water with vegetation.

Tendipes riparius (Meigen)—11♂♂, 20♀♀ (2 : 0 : 0 : 0 : 29); April 24-May 16, maximum April 26 (6 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) where it emerged also later in the season.

Tendipes dux (Joh.)—23♂♂, 33♀♀ (2 : 14 : 0 : 0 : 40); May 8-August 12, maxima May 9, July 22 (3, 4 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b) and at London (Judd, 1957a) and South Walker Pond (Judd, 1960).

Tendipes nervosus (Staeger)—114♂♂, 237♀♀ (45 : 105 : 43 : 8 : 150); April 30-September 9, maxima May 1, July 3 (17, 37 insects), Figure 3. This species was trapped also in 1956 from Redmond's Pond (Judd, 1958b).

Glyptotendipes lobiferus (Say)—179♂♂, 72♀♀ (197 : 1 : 0 : 0 : 53); April 4-July 14, maxima April 28, May 24 (11, 74 insects), Figure 3. This species was also trapped commonly in the Dundas Marsh (Judd, 1953), at London (Judd, 1957a) and at South Walker Pond (Judd, 1960). Its heavy emergence in Traps 1 and 5 on Redmond's Pond indicates that the larvae dwell in shallow water about vegetation.

Glyptotendipes brachialis (Coq.)—47♂♂, 43♀♀ (2 : 51 : 3 : 31 : 3); May 8-September 14, maximum June 26 (6 insects), Figure 3. This species was also trapped at London (Judd, 1957a) and South Walker Pond (Judd, 1960) where it likewise showed a maximum emergence at the end of June. In Redmond's Pond it emerged mostly in the open water at Traps 2 and 4.

Microtendipes pedellus (DeGeer)—59♂♂, 14♀♀ (4 : 0 : 4 : 12 : 53); April 28-September 1, maximum July 10 (5 insects), Figure 3. This species was also trapped on South Walker Pond (Judd, 1960).

Tendipes sp.—39♀♀ (2 : 37 : 0 : 0 : 0); June 24-September 22.

Calopsectra sp.—167♂♂, 5,839♀♀ (156 : 134 : 289 : 130 : 5,297); April 24-October 4, maxima April 25, May 31, July 6 (97, 369, 291 insects), Figure 4. These small, green midges emerged throughout the season. Their preponderance at Trap 5 indicates that the larvae dwell about vegetation in shallow water.

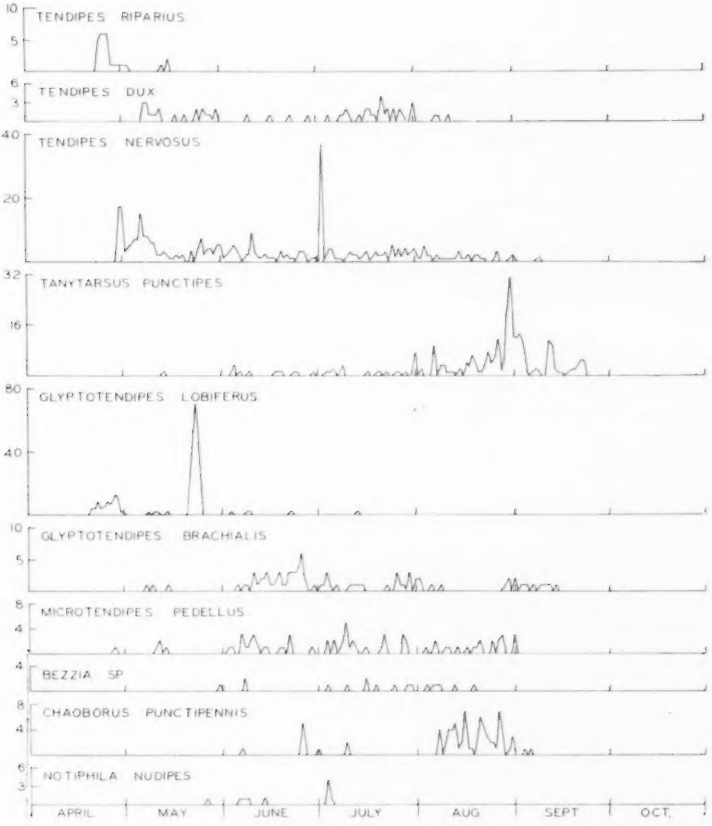

Fig. 3.—Periods of emergence of adult insects

CERATOPOGONIDAE

Alluaudomyia bella (Coq.)—1♀ (0 : 0 : 0 : 1 : 0); August 24. Larvae of this species have been found by Thomsen (1937) in algae, dead leaves and mud from ponds and swamps.

Culicoides (*?piliferus* R. and H.) (USNM)—1♀ (0 : 0 : 1 : 0 : 0); June 2. *C. piliferus* was trapped also in June on South Walker Pond in 1956 (Judd, 1960).

Atrichopogon sp.—2♂♂, 7♀♀ (3 : 0 : 0 : 6 : 0); June 12-26, August 26-31. The period of emergence recorded here for *Atrichopogon* is similar to that found by Judd (1960) at South Walker Pond where the flies emerged in late June and July and again in August and September.

Bezzia sp.—5♂♂, 12♀♀ (0 : 0 : 12 : 2 : 3); May 31-August 12, Figure 3. Midges of this species were also trapped at South Walker Pond (Judd, 1960).

Other Heleidae—19 midges (5 : 3 : 1 : 8 : 2); May 31-September 11.

CULICIDAE

Chaoborus flavicans (Meigen)—1,475♂♂, 1,225♀♀ (394 : 263 : 902 : 170 : 971); April 23-September 27, maxima April 27, June 5, July 31 (83, 289, 34 insects), Figure 4. This species was trapped also in 1956 on Redmond's Pond (Judd, 1958b) when it likewise showed its maximum emergence in June. Its preponderance at Traps 1, 3 and 5 indicates that the adults emerge mainly from shallow water. The species was trapped at London (Judd, 1957a) and South Walker Pond (Judd, 1960).

Chaoborus punctipennis (Say)—45♂♂, 30♀♀ (0 : 33 : 14 : 13 : 15); June 7-September 6, maximum August 27 (7 insects), Figure 3. Only one specimen was trapped on Redmond's Pond in 1956 (Judd, 1958b). Most of the adults emerged from the more open water at Traps 2 and 4. This species was also trapped at London (Judd, 1957a) and at South Walker Pond (Judd, 1960).

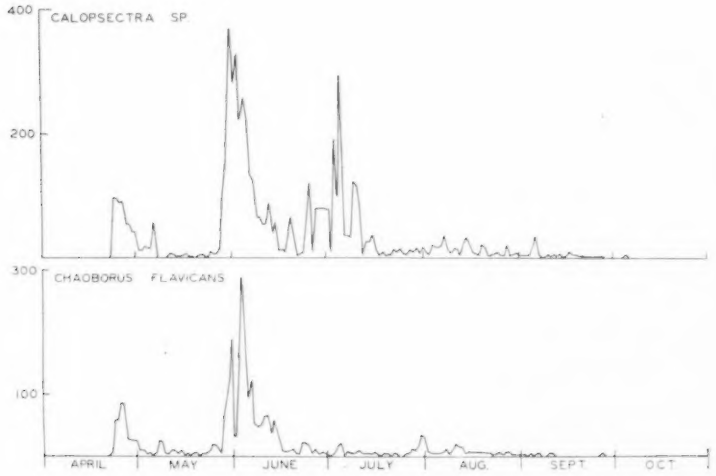

Fig. 4.—Periods of emergence of adult insects

DOLICHOPODIDAE

Dolichopus albiciliatus Lw.—1♀ (0 : 0 : 0 : 0 : 1) (CNC); June 7. Several other species of *Dolichopus* have been trapped from bodies of water in the vicinity of London (Judd, 1957a and 1960).

Gymnopternus barbatulus Lw.—1♀ (0 : 0 : 0 : 0 : 1) (CNC); July 10. This species was also trapped in July, 1954 from a pool at London (Judd, 1957a).

SIMULIIDAE

Simulium vittatum Zett.—1♂, 6♀♀ (5 : 1 : 0 : 0 : 1); June 11-September 6. This species was collected also in 1956 in the Byron Bog by sweeping the bushes in the *Chamaedaphnetum calyculatae* association which surrounds Redmond's Pond (Judd, 1957c). Its first emergence in the trap in 1957, June 11, was eighteen days earlier than the date of its first collection, June 29, in the sweeping in 1956.

TABANIDAE

Chrysops montana O.S.—1 deer-fly (0 : 0 : 0 : 1 : 0); June 4. This species was not among the tabanids collected in the Byron Bog in 1956 (Judd, 1958a). It has been recorded at Algonquin Park in Ontario where it was first found in flight on June 16 (Davies, 1959).

EPHYDRIDAE

Notiphila nudipes Cresson—2♂♂, 9♀♀ (0 : 0 : 0 : 0 : 11) (5, CNC); May 27-July 5, Figure 3. Berg (1949) found larvae of *N. loewi* on the roots of *Potamogeton* and McGaha (1952) found the same species associated with flowers of the water-lilies *Nymphaea odorata* and *N. tuberosa*. In Redmond's Pond *N. nudipes* may have been associated with spatter-dock, *Nuphar advena*, for all the flies emerged in Trap 5 which had this plant in it.

MUSCIDAE

Coenosia tigrina Fab.—1 fly (0 : 0 : 0 : 0 : 1); July 28. Under the subfamily Coenosiinae Usinger *et al.* (1956) list a few species of flies with aquatic larvae but do not include any in the genus *Coenosia*.

REFERENCES

ALEXANDER, C. P. 1942. Family Tipulidae. The Diptera or true flies of Connecticut. *Conn. State Geol. Nat. Hist. Surv. Bull.*, **64**:196-486.

BERG, C. O. 1949. Limnological relations of insects to plants of the genus *Potamogeton*. *Trans. Am. Microscop. Soc.*, **68**:279-291.

DAVIES, D. M. 1959. Seasonal variation of tabanids (Diptera) in Algonquin Park, Ontario. *Can. Entomol.*, **91**:548-553.

JUDD, W. W. 1953. A Study of the population of insects emerging as adults from the Dundas Marsh, Hamilton, Ontario, during 1948. *Am. Midl. Nat.*, **49**:801-824.

———1957a. A study of the population of emerging and littoral insects trapped as adults from tributary waters of the Thames River at London, Ontario. *Ibid.*, **58**:394-412.

———1957b. Studies of the Byron Bog in southwestern Ontario. I. Description of the bog. *Can. Entomol.*, **89**:235-238.

———1957c. Studies of the Byron Bog in southwestern Ontario. IV. Seasonal distribution of the black fly, *Simulium vittatum* Zett. (Diptera : Simuliidae). *Entomol. News*, **68**:263-265.

———1958a. Studies of the Byron Bog in southwestern Ontario. V. Seasonal distribution of horseflies and deerflies (Tabanidae). *Can. Entomol.*, **90**: 255-256.

———1958b. Studies of the Byron Bog in southwestern Ontario. IX. Insects trapped as adults emerging from Redmond's Pond. *Ibid.*, **90**:623-627.

———1960. A study of the population of insects emerging as adults from South Walker Pond at London, Ontario. *Am. Midl. Nat.*, **63**:194-210.

KRAATZ, W. C. 1918. *Scirtes tibialis*, Guer., (Coleoptera-Dascyllidae), with observations on its life history. *Ann. Entomol. Soc. Am.*, **11**:393-401.

MCGAHA, Y. T. 1952. The limnological relations of insects to certain aquatic flowering plants. *Trans. Am. Microscop. Soc.*, **71**:355-381.

ROSS, H. H. 1944. The caddisflies, or Trichoptera, of Illinois. *Bull. Illinois Nat. Hist. Surv.*, **23** (Article 1). 326 pp.

THOMSEN, L. 1937. Aquatic Diptera. Part V. Ceratopogonidae. *Mem. Cornell Univ. Agric. Exp. Stn.*, **210**:57-80.

USINGER, R. L., ET AL. 1956. *Aquatic Insects of California with Keys to North American Genera and California Species*. Univ. California Press, Berkeley. 508 pp.

WALKER, E. M. 1953. *The Odonata of Canada and Alaska*. Vol. I. University of Toronto Press, Toronto. 292 pp.

———1958. *The Odonata of Canada and Alaska*. Vol. II. University of Toronto Press, Toronto. 318 pp.

WOOLVERTON, S. 1900. Report of the geological section. *Thirtieth Ann. Rep. Entomol. Soc. Ont.* (1899):45-47.

The Comparative Morphology of the Definitive Swim Bladder in the Catostomidae

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ABSTRACT: The definitive swim bladder of the Catostomidae has been described and its variations noted. It is characteristically the two-chambered type found in cypriniform fishes in general and described by Tracy as Group 2.

The anterior chamber is encased in a tunica externa made up of special connective tissue fibers. This tunic is in two layers and the fibers of these layers are arranged at right angles to each other. It is proposed that this arrangement prevents over-expansion of the anterior chamber and thus maintains free range-of-motion for the Weberian ossicles.

The usual catostomid swim bladder is 35 - 45 per cent of the standard length of the individual. *Hypentelium*, adapted to riffle-type life, has the posterior chamber somewhat reduced. *Thoburnia* and *Pantosteus*, adapted to mountain streams, have the posterior chamber even more reduced.

The *Moxostoma* genus-group (*Moxostoma*, *Placopharynx*, *Megapharynx* and *Lagochilia*) has a three-chambered swim bladder. *Thoburnia* and *Hypentelium* are retained as separate genera of the Moxostomatini, being more primitive, although specialized, than the former.

Introduction

The Catostomidae is a family of teleost fishes, the suckers, in the cypriniform subdivision of the Ostariophysi. The catostomid fishes comprise some fifteen or seventeen genera and about a hundred species. For the most part they are limited to the fresh-waters of North America extending as far south as the Mexican Highlands. One genus, *Myxocyprinus*, however, is restricted to the fresh-waters of Central China from Szechwan to Fukien Provinces. A subspecies of the northern sucker, *Catostomus catostomus rostratus*, has invaded northeastern Siberia where it is to be found in the fresh-waters of the Kamchatka Peninsula and westward to the Lena River.

The typical cypriniform swim bladder is a two-chambered structure found in the body cavity (Fig. 1.). It lies immediately beneath the vertebral column in a retroperitoneal space above the abdominal viscera. A pneumatic duct passes along with the "service tissues" (vessels and nerves) between the two leaves of the dorsal mesentery and connects the posterior chamber of the swim bladder to the anterior gut. The anterior chamber is connected to the posterior by an inter-chamber duct and to the inner ear by an ossicle chain, the Weberian ossicles characteristic of the ostariophysine fishes. The definitive swim bladder of cypriniform fishes develops in a characteristic manner from an initial dorsal outgrowth of the gut wall (Nelson, 1959).

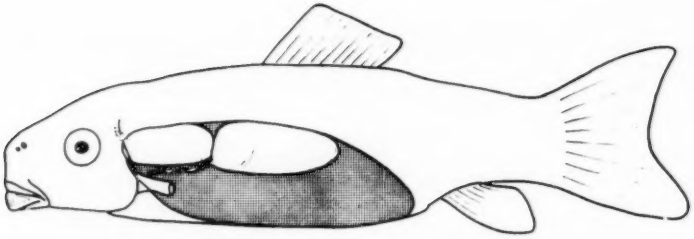


Fig. 1.—A schematic representation of the swim bladder *in situ* in *Catostomus commersoni*.

Since the swim bladder is usually a gas-filled structure, it plays an important role in the bouyancy of the individual fish. Different habitats place different requirements for survival upon the species, through the individual, and the swim bladder is responsive to the varying bouyancy requirements of different aquatic environments. Secondary roles are also possible for the swim bladder. In the Ostariophysi as a group, the anterior chamber has the added function of vibration reception and transmission to the membranous labyrinth to improve the sense of "hearing."

Within the Catostomidae the swim bladder has long been recognized as being a useful taxonomic tool because of its basic variation among the genus-groups. Hubbs (1930) used the number of chambers of the catostomid swim bladder as a primary character in his "Key to the Genera." Most recently, Robins and Raney (1956, 1957) made judgments as to the proper placing and synonomy of various species of catostomids on the same basis.

Many individual references to the swim bladders of individual species of catostomids have been made in the literature. No really complete or systematic morphology study of the swim bladder in the Catostomidae has been made to date, however. Dobbin (1941) gave very brief descriptions of the swim bladder in six species from five genera and figured three with outline sketches. The object of the present paper is to treat the swim bladder in the entire family in a systematic and more-or-less complete fashion as part of an over-all study of the Catostomidae. Fifty-two species, including representatives of all genera, have been examined in this study. All references to size or length are for standard length.

I express my thanks to the many people and institutions whose courtesies and help over the years have made this study possible. The majority of the specimens came from the Wisconsin Conservation Department, the University of Michigan Museum of Zoology, Chicago Natural History Museum, United States National Museum, Academy of Natural Sciences of Philadelphia and the Museum of Comparative Zoology. A number of separate items were made available to me by many persons, too numerous to mention individually, but whose action is much appreciated.

MORPHOLOGICAL FINDINGS

Chambers of the Swim Bladder.—The swim bladder in catostomid fishes may be either a two-chambered or three-chambered structure. The genus-group of *Moxostoma* is characterized by having the three-chambered type of swim bladder while all of the other genera have the two-chambered type. As presented in a previous paper (Nelson, 1959), the posterior chamber develops from the single chamber of the primitive swim bladder. The anterior chamber develops from a primordium which grows out from the anterior surface of this single chamber. Therefore, the swim bladder of catostomids is characterized as being in Tracy's (1911) Group 2.

The anterior and posterior chambers are inter-connected by an inter-chamber duct. This duct is located centrally on the opposing surfaces of the two chambers. It is distinctly separate from the pneumatic duct which opens into the lower anterior surface of the posterior chamber and connects the posterior chamber with the esophagus.

The third chamber of the moxostomids is connected to the second by a dorsal inter-chamber duct. This connection is a sometimes broader than a mere duct. The age at which the third chamber is acquired must be very early since even specimens of 2.5 cm have it.

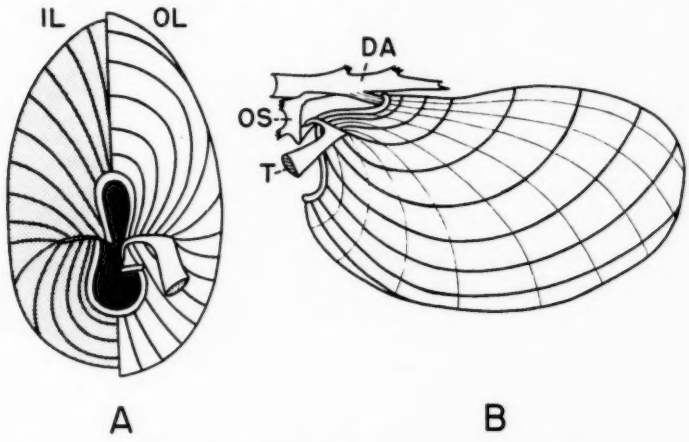


Fig. 2.—A schematic representation of the tunica externa of the catostomid swim bladder. A. Dorsal view with the anterior end at bottom. On the right side is depicted the lines of the direction of the fibers of the outer layer (OL). On the left side the outer layer has been removed to show the direction of the fibers of the inner layer (IL). The transformator process of the tripus is *in situ* attached to the outer layer. B. Lateral view to show the arrangement of the fibers of the inner and outer layers being at right angles to each other. The outer layer and transformator process (T) are attached to the suspensorium (OS) and the dorsal aorta (DA) gives off branch to the anterior chamber where the tunica interna is exposed at the central opening of the tunica externa.

In these very small specimens (2.5 and 3.8 cm), however, the third chamber is relatively smaller in size than usual.

Chamber Walls.—Fänge (1953) has presented a satisfactory resumé of the thinking concerning the layers of the swim bladder walls. In the catostomids the lumen of the swim bladder as a whole is lined by a continuous layer of epithelium. Next to this thin layer of epithelium is a layer of intermingled nonstriated muscle and connective tissue fibers. Three zones are apparent in this second layer: a) an inner zone primarily of connective tissue fibers; b) a thick zone which is the main area of the circular muscle fibers; and, c) an outer zone which is again mainly of connective tissue fibers. These two layers, epithelial and muscular, make up the tunica interna of the anterior chamber.

The tunica externa of the anterior chamber is formed of two thick layers of white connective tissue fibers. Each layer has all of its fibers arranged parallel so that one can produce long narrow splits in a layer with a dissecting needle. Figure 2 diagrams the manner in which the fibers of the inner and outer layers tend to always be coursing at right angles to each other (similar to the fibers of the intercostal and abdominal oblique musculature). Between the external and internal tunics of the anterior chamber is a loose connective tissue which allows these two tunics to be easily separated from one another.

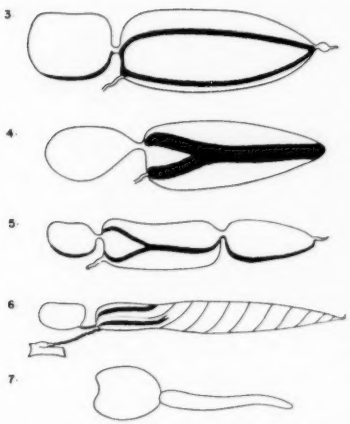
The posterior chamber has a single wall. This represents essentially a fusion of all layers into the single structure.

Posterior Extensions of the Posterior Chamber.—In certain genera of catostomids an extension arising from the posterior end of the posterior-most chamber is to be seen frequently. The lumen of this extension is continuous with that of the swim bladder proper. The posterior extension may have a simple tubular form or may be a bulbous enlargement, as if it were a miniature additional chamber.

The tubular type of posterior extension may be seen in *Carpiodes, Ictiobus, Megastomatobus, Moxostoma, Placopharynx* and *Cycleptus.* It may be short or of varying length, sometimes quite long as in *Moxostoma.* This tubular extension may be folded dorsally or ventrally; it may be straight posteriorly; or, it may be slightly convoluted. In all cases, however, it is usually embedded in the loose fascia filling the retroperitoneal space behind the swim bladder.

The bulbous type of extension, as far as the specimens available are concerned, is limited to the *Carpiodes* and *Moxostoma.* It is particularly evident in the former.

Longitudinal Bands.—Paired longitudinal bands occur on the lateral aspects of the posterior chamber wall of the catostomid swim bladder. These bands represent thickenings of the muscle or connective tissue fiber masses. In *Carpiodes* (Fig. 3), *Ictiobus, Megastomatobus, Cycleptus* (Fig. 6), and *Myxocyprinus* these longitudinal bands are muscular and doubled, one band dorsal and the other ven-



Figs. 3-7. Variation in swim bladders of catastomid fishes. 3. *Carpiodes cyprinus*, the type seen in the ictiobids, lateral view. 4. *Minytrema melanops*, lateral view. 5. *Moxostoma aureolum*, the type seen in the moxostomids, lateral view. 6. *Cycleptus elongatus*, lateral view. Note the triple spiralling of the two pairs of longitudinal bands. 7. *Thoburnia rhothoeca*, dorsal view. This is an example of the reduced type of swim bladder.

tral along the length of the posterior chamber converging towards the posterior end.

In *Catostomus, Erimyzon, Minytrema* (Fig. 4), *Moxostoma* (Fig. 5) and *Placopharynx* it appears as if these two bands (as seen above) have become variously fused so that there is a single longitudinal band on each side of the posterior chamber wall. The anterior end of this single band remains doubled to varying distance so as to have the appearance of a "Y" lying on its side. In *Catostomus*, however, it is not at all uncommon to find this band to be single throughout its entire length.

Spiral Character.—Several genera of catostomids exhibit a spiral "twisting" of the longitudinal bands of the posterior chamber in about ten per cent of the specimens. *Cycleptus* (Fig. 6) demonstrates this morphological character to the maximum degree. Here the anterior portion of the posterior chamber has the double muscular bands between which are longitudinal bands of thickened fibrous connective tissue. The latter produce internal ridges on the wall of the posterior chamber and are seen externally as grooves. In the posterior three-quarters of the posterior chamber the muscle bands are no longer apparent but the fibrous bands become spiralled into three complete turns.

The description above of the *Cycleptus* swim bladder is that for the definitive bladder. In a series of thirteen specimens, sizes 3.28 to 57.0 cm, the progressive development of this condition is demonstrated. In the youngest specimens the posterior chamber is simple and without any special modifications. Between the 6 to 9 cm sizes a single turn of fibrous bands may be seen along the entire length of the posterior chamber. The time at which the second and third turns appear cannot be ascertained in this limited series of specimens. The definitive bladder may at times also show the fiber bands twisted

along the entire length of the posterior chamber and one large specimen had only two instead of three turns.

In *Carpiodes* the spiralling extends into the bulbous posterior extension where it is quite marked. In *Moxostoma* the spiralling is limited to the third, the posterior-most chamber.

Those swim bladders of *Carpiodes* and *Ictiobus* which have this spiral character all have the direction of twist counter-clockwise when viewed from behind. The twist of the bands in *Megastomatobus*, *Cycleptus* and *Moxostoma* are all clockwise when viewed from behind.

Relationships of the Swim Bladder Length to the Standard Length of the Body.—The swim bladder of catostomid fishes occupies from a third to almost a half of the length of the body of the fish (Table I). It remains within the limits of the body cavity without extending posteriorly into the caudal portion of the body. In certain species the swim bladder is reduced in length to varying degrees. In *Thoburnia atripine* and *Hypentelium nigricans* the swim bladder is about a fourth of the body length. This is also true of the genus *Pantosteus* in general. In *Thoburnia rhothoeca* and *Pantosteus santa-anae* the

TABLE I.—Ratios of the swim bladder length/standard body length in the Catostomidae

	SB/SL × 100 = %	Number of Specimens: Measured	Examined
Cycleptinae:	(43.9)		
Cycleptus	44.5	4	13
Myxocyprinus	42.6	2	2
Ictiobinae:	(39.7)		
Carpiodes	40.3	13	49
Ictiobus	38.3	5	9
Megastomatobus	39.0	2	31
Catostominae:			
Catostomini:	(35.0)		
Catostomus	35.2	26	126
Chasmistes	32.1	2	3
Xyrauchen	36.0	1	1
Moxostomatini:	(44.2)		
Moxostoma (less *mascotae*)	44.1	14	52
Placopharynx	43.1	3	4
Lagochila	45.2	4	4
Erimyzonini:	(36.1)		
Erimyzon	35.5	8	20
Minytrema	38.3	5	36
"Reduced Swim Bladders":			
Moxostoma mascotae	38.8	22	22
Thoburnia atripinne	28.1	9	9
Hypentelium nigricans	27.9	11	16
Thoburnia rhothoeca	17.2	14	16
Pantosteus (less *santa-anae*)	22.1	7	24
Pantosteus santa-anae	13.8	3	5
		155	444

swim bladder is even more reduced in length. In not a single specimen was the swim bladder found to be absent! (In *Thoburnia rhothoeca* the swim bladder is so small and buried in the fat and head-kidney tissue that it can be easily overlooked.) In all instances of reduced length, the posterior chamber undergoes the main reduction whereas the anterior chamber is relatively unaltered.

The question of possible shrinkage of the swim bladder during preservation was recognized as having possible consequences in this particular phase of this study and a simple experiment was performed to obtain some ideas about this matter. Fresh frozen specimens of *Catostomus commersoni* were used. During the removal of the swim bladder of the first specimen it was noted that the bladder contracted slightly when the pneumatic duct was transsected. The second bladder was therefore filled with the fixing solution before removal from the body. Both swim bladders were removed from the fishes and placed into a calcium-formal fixing solution. After two and a half weeks they were transferred to seventy per cent ethyl alcohol for storage. In both cases the shrinkage of the anterior chamber was about fifteen per cent while that for the posterior chamber was about ten per cent of the freshly removed swim bladders. All of the shrinkage was completed by the time the specimens were placed in the alcohol since subsequent measurements for a period of three months showed no appreciable change. The SB/SL ratio changed from about forty per cent in the fresh state to about thirty-five per cent in the preserved state. This latter figure agrees well with the figure obtained from museum specimens. Thus it is assumed that all of the museum specimens have undergone the same amount of shrinkage uniformly and the ratios in Table I are those taken directly from the museum specimens.

When the swim bladder lengths of the various genera are plotted against standard lengths on plain graph paper, the resulting progression lines are essentially straight lines. The slope of these lines averages about twenty degrees. The few very large specimens (i.e. an adult *Myxocyprinus* of almost a meter in length) tend to flatten the end of the line towards a plateau.

DISCUSSION AND CONCLUSIONS

The Chambers of the Swim Bladder.—The two-chambered swim bladder is characteristic for the Catostomidae. Also, from both morphological and developmental studies it is apparent that the swim bladder seen in the Catostomidae is the same as for the other families of the cypriniform group of ostariophysines. This type of swim bladder has a posterior chamber with a single wall and is connected to the anterior gut via the pneumatic duct. The anterior chamber has a tunica interna which is continuous with the wall of the posterior chamber. About this inner tunic is consolidated a thick fibrous capsule, the tunica externa. The tunica externa is readily separated from the tunica interna by virtue of a loose connective tissue between them.

The presence of a third chamber in the moxostomatids is a mor-

phological fact but its significance is enigmatic. This situation apparently reresents a constriction of the normal posterior chamber since the pneumatic duct connects with the second chamber precisely as is the case with the posterior chamber of the two-chambered swim bladder. Also, the dorsal inter-chamber duct between the second and third chambers is on occasion large and fails to exhibit the characteristics usually associated with true ducts. It may be of systematic significance in that only those genera closely related as a *Moxostoma* group (*Moxostoma, Placopharynx, Megapharynx,* and *Lagochila*) possess this characteristic, whereas, other genera which exhibit structural affinity, Weberian apparatus and opercular series (Nelson, 1948, 1949), with this genus-group (*Thoburnia* and *Hypentelium*) have only the regular two-chambered bladder. Thus, we can agree with Robins and Raney (1956) and Bailey (1959) in considering all of the genera of the *Moxostoma* group as being subgenera of the genus *Moxostoma,* but retain *Thoburnia* and *Hypentelium* as separate and more primitive genera of the tribe Moxostomatini for the time being.

The literature has occasionally implied the presence of a third chamber on the swim bladder of *Minytrema,* and hence a close relationship to *Moxostoma.* In the present study the swim bladders of *Minytrema* and *Erimyzon,* Erymzonini, were consistent in being only two-chambered and well-rounded posteriorly; there is not the slightest indication of a possible posterior extension, much less an additional chamber. This type of swim bladder is morphologically much more similar to that of the Catostomini than to any other catostomid group.

Not a single specimen in this series of catostomids showed an absence of the swim bladder. The literature has reported occasionally that the swim bladder of *Thoburnia rhothoeca* was lacking in adult specimens. This is probably based upon the anatomical fact that in this genus the swim bladder is much reduced and is frequently actually buried in the retroperitoneal tissue of the dorso-anterior portion of the body cavity.

The Tunica Externa of the Anterior Chamber.—The anterior chamber of the catostomid swim bladder appears to be specially adapted to function as a sound-wave receptor and to transmit these vibrations to the inner ear via the Weberian ossicle chain. The tunica externa forms a strong fibrous capsule about the gas-filled tunica interna and is attached to the Weberian apparatus, both at the ossa suspensoria and the transformator processes of the two tripuses. Because of the lack of adequate experiments with living fishes we may presume that the arrangement of the heavy connective tissue fibers of the two layers of the tunica externa at right angles to one another is a special adaptation for limiting possible over-expansion of the anterior chamber. (Expansion of the anterior chamber would occur with each ascent of the fish in its aquatic medium since the ascension would result in a reduction of the ambient pressure thus allowing an increased volume to the enclosed gases according to Boyle's Law. The posterior chamber, by means of the pneumatic duct and its valvular

mechanism in the wall of the esophagus, retains the bouyancy regulation function for the fish.) Too extensive expansion of the diameters of the anterior chamber would negate the functioning of the ossicle chain by limiting the range-of-motion of the normal articulations of the tripus and claustrum to the vertebrae.

Posterior Extensions.—Previously (Nelson, 1959), I noted that during the growth phase of the posterior chamber, a "nipple"-like posterior extension was present which retained the cytoarchitectural characteristics of the original diverticulum from the dorsal gut wall. These posterior extensions found in the definitive swim bladders may then be looked upon as resulting from an over-functioning of the organizing potential of the swim bladder determining mechanism to the extent that additional swim bladder structure is produced over and beyond the normal swim bladder morphology. This would be particularly true in the case of *Carpiodes* where the bulbous type of posterior extension gives the appearance of an additional, miniature chamber, even to the inclusion of the spiralling characteristic of the longitudinal bands.

Spiralling.—Except for *Cycleptus* this morphological character occurs sporatically (about ten %) rather than consistently. Moreover, it is a character which is not limited to a catostomid swim bladder but has been observed in other studies on the swim bladders of characins and gymnotids. How this "twisting" comes about (the swim bladder definitely does not rotate in place) and what it means in the economy of the fish is completely unknown.

Longitudinal Bands.—The thickening of muscle and/or connective tissue fibers into longitudinal bands represents a specialization in the swim bladders of the Catostomidae. The functional significance of these bands is not apparent from these studies but requires physiological experimentation with living material. We can, however, presume that the double condition seen in the genera of the subfamilies Cycleptinae and Ictibobinae represent the simpler and more primitive condition. The partially fused "Y" or completely fused single bands found in the Catostominae would then represent an increase complexity of morphology and thus place them at a higher systematic level.

Relationships of the Swim Bladder Length to the Standard Length of the Body.—A number of investigators have noticed that a fresh-water fish which is habitually suspended in the water medium possesses a swim bladder which is about seven per cent of the total body volume. The majority of the catostomid fishes can be classed in this category, albeit they are usually suspended just above the bottom. The small variation of the SB/SL ratios from thirty-five to forty-five per cent reflects only the differences in depth and width of the various swim bladders.

On the other hand, the genus *Hypentelium* is adapted to the more turbulent conditions of stream riffles while the genus *Thoburnia* is adapted to the swifter flowing waters of the mountain streams of the

Alleghenies in eastern North America and the genus *Pantosteus* similarly to the mountain streams of the Rockies in western North America. Apparently the species *Moxostoma mascotae* in the Highlands of Mexico parallels *Hypentelium* (Robins and Raney, 1957). In a series of twenty-two specimens of *M. mascotae* in two lots from the Rio Ameca and Rio Mascota, the SB/SL ratio is about thirty-eight per cent as compared to about forty-three per cent found in the *Moxostoma* group in general. *Thoburnia atripine* and *Hypentelium nigricans* both have ratios of twenty-eight per cent. The genus *Pantosteus* is similar. In all of these forms, the bouyancy controlling portion of the swim bladder (the posterior chamber) is the part mainly reduced and these forms are able thereby to maintain themselves better in position despite the faster flowing waters of their habitats. The acme of this specialization to swift waters is to be seen in the species *Thoburnia rhothoeca* and *Pantosteus santa-anae* where these ratios are much smaller.

The progression line of the plotted swim bladder lengths against the standard lengths of the body lead to two interesting conclusions. The fact that this line is essentially a straight line demonstrates that the growth of the swim bladder in relation to the growth of the body length is of the orthometric type. The fact that the slope of this line is approximately twenty degrees indicates that the SB/SL ratio begins and remains somewhere between thirty-five and forty per cent.

REFERENCES

BAILEY, REEVE M. 1959. A new catostomid fish, *Moxostoma* (*Thoburnia*) *atripinne*, from the Green River drainage, Kentucky and Tennessee. *Occ. Pap. Mus. Zool. Univ. Mich.*, **559**:1-19.

DOBBIN, CATHERINE N. 1941. A comparative study of the gross anatomy of the air-bladders of ten families of fishes of New York and other eastern states. *J. Morphol.* **68**:1-29.

FÄNGE, RAGNAR 1953. The mechanisms of gas transport in the euphysoclist swimbladder. *Acta Physiol. Scand.*, **30**, Suppl. No. 110.

HUBBS, CARL L. 1930. Materials for a revision of the catostomid fishes of eastern North America. *Misc. Publ., Mus. Zool. Univ. Mich.*, **30**:1-47.

NELSON, EDWARD M. 1948. The comparative morphology of the Weberian apparatus of the Catostomidae and its significance in systematics. *J. Morphol.*, **83**:225-251.

1949. The opercular series of the Catostomidae. *J. Morphol.* **85**:559-567.

———1959. The embryology of the swim bladder in the common sucker, Catostomus commersoni (Lacopede). *Am. Midland Nat.*, **61**:245-252.

ROBINS, C. RICHARD AND EDWARD C. RANEY. 1956. Studies of the catostomid fishes of the genus *Moxostoma*, with descriptions of two new species. *Mem. Agr. Exp. Sta., Cornell Univ.* No. **343**:1-56.

——— AND ———1957. The systematic status of the suckers of the genus *Moxostoma* from Texas, New Mexico and Mexico. *Tulane Stud. Zool.*, **5**:291-318.

TRACY, HENRY C. 1911. The morphology of the swim-bladder in teleosts. *Anat. Anz.* **38**:600-606.

Distribution of Some Mexican Fungi in North America

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ABSTRACT: When North America is divided into eight floristic regions roughly correlated with the distribution of woody angiosperms and conifers, a noticeable correspondence is found with the distribution of Polyporales. Twenty-seven species of Mexican Thelephoraceae and thirty-seven species of Mexican Polyporaceae are compared with reports of these same species from the other North American regions. By means of such reports, the affinities of these regions with Mexican mycota is shown.

Any attempt to discuss the geographical distribution of fungi is severely limited by the distressing lack of regional monographs and collections, by misinterpretations, and the erratic seasonal appearance of many species. When attempting to plot the distribution of saprobic fungi, these factors are especially intensified. Nevertheless, we have undertaken a modest discussion of the distributional affinities of some Mexican Thelephoraceae and Polyporaceae in relation to North America as a whole.

Bisby (1933; 1943) has reviewed the literature of fungus geography until 1943; the majority of the geographical studies have been upon plant pathogens, particularly those attacking crop plants. The few reports that exist on the distribution of saprobic fungi, such as those of Overholts (1939) and Lange (1934), have been chiefly concerned with North American and European fungi. Bisby (1933) and Lange are agreed that probably less distinction exists between temperate species of the eastern and western hemispheres than between those from northern and southern regions. Such studies as those of Bisby, Reichert (1921), and Sharp (1948) represent the very few reports on the distribution of tropical and subtropical species. No doubt, this represents a lack of knowledge of tropical forms rather than a lack of interest. Comparisons of tropical and subtropical species with those of temperate regions should prove to be of utmost interest as more information is accumulated through additional collections from warmer regions.

Fully cognizant of the difficulties mentioned, we have compared sixty-two species of Mexican fungi with distributional reports of various authors, primarily Burt (1914-1926), Murrill (1907; 1912; 1915), and Overholts (1953). These Mexican specimens were collected by us, and, in many cases, checked by recognized authorities. The taxonomic account of these fungi appears elsewhere (1960).

For convenience we have divided North America into eight regions (Fig. 1). These regions correspond roughly to the distribution of hardwoods and conifers — based primarily on Harshberger's work as shown in the maps of Goodall and Darby (1953). In many instances these regions also follow natural geographical or physiographical divisions; in others it has been more practicable to follow political boun-

daries. Further refinement and shifting of regional lines is both inevitable and desirable. Certain areas, *e.g.*, the New Mexico and Arizona highlands, assigned to a given region, may well be considered to belong to another. Similarly, the Gulf Coast which is here included

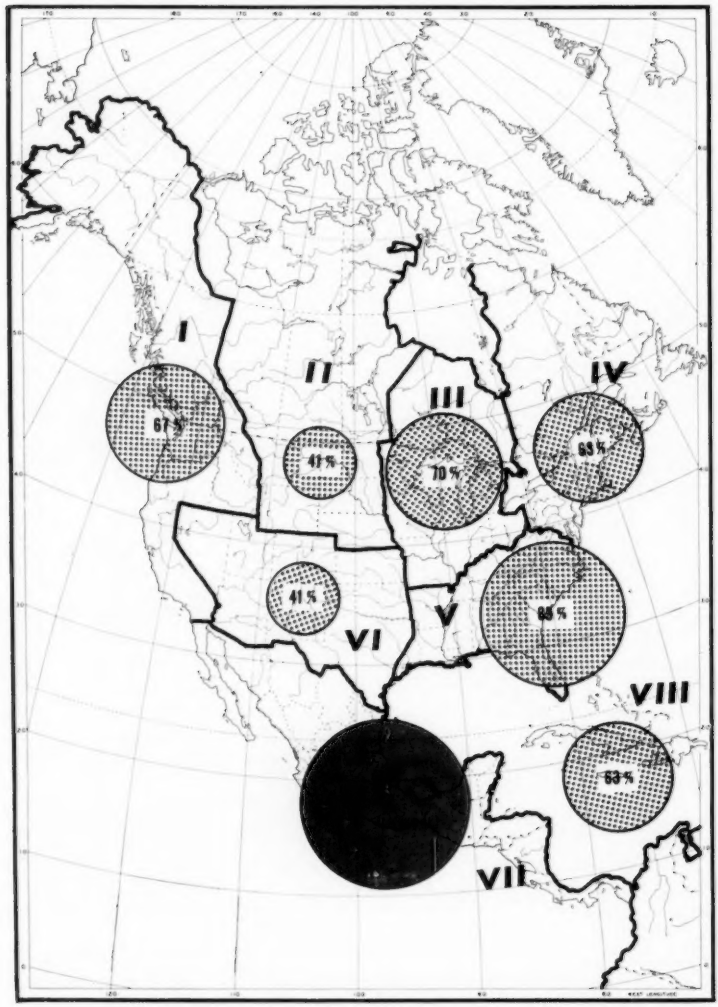

Fig. 1.—A comparison of the percentage of Mexican Thelephoraceae (dark circle representing 100%) found in the remaining regions of North America. Based on a collection of 27 Mexican thelephores, comparisons are valid only between Region VIII and the other regions.

in Region V might well be an independent region or subregion. However, for the present discussion and for reasons previously cited, it seems better to ignore such problems.

Region I includes Alaska (perhaps only the Pacific coast of Alaska belongs here), Yukon, British Columbia, Washington, Oregon, California, Idaho and western Montana. Region II consists of the Northwest Territories, Alberta, Saskatchewan, Manitoba, central and eastern Montana, North and South Dakota, Wyoming, and Nebraska. Region III includes Ontario (except the southeastern portion), Wisconsin, Minnesota, Michigan, Iowa, Missouri, Illinois, Indiana, and Ohio. Region IV includes southeastern Ontario, Quebec, Labrador, New Brunswick, Nova Scotia, and the New England and Middle Atlantic states. Region V is the southeastern United States from the Virginias, Kentucky, and Arkansas south to the Gulf of Mexico and west to eastern Texas. Region VI is formed by central and west Texas, west along the Mexican border to the Great Basin states and north to the northern borders of Kansas and Colorado. Region VII is Central America. Region VIII represents the West Indies (excluding Trinidad and its satellites as belonging floristically as well as physiographically to the South American mainland).

TABLE I.—Distribution of certain Mexican Thelephoraceae in North America

Species	Region							
	I	II	III	IV	V	VI	VII	VIII
1. *Aleurodiscus griseo-canis*			×					
2. *Coniophora olivacea*	×	×	×	×	×			
3. *Cora pavonia*					×		×	×
4. *Corticium lactescens*	×		×	×	×		×	×
5. *Corticium pelliculare*	×		×	×		×	×	×
6. *Corticium portentosum*	×		×	×	×		×	×
7. *Corticium sphaerosporum*				?	×			
8. *Cotylidia cyphelloides*								×
9. *Hymenochaete pinnatifida*					×		×	×
10. *Hymenochaete tabacina*	×	×	×	×	×	×	×	
11. *Pellicularia vaga*	×	×	×	×	×	×	×	
12. *Peniophora byssoides subsp. tomentella*					×		×	
13. *Peniophora cinerea*	×	×	×	×	×	×	×	×
14. *Peniophora roumeguerii*	×		×		×			×
15. *Peniophora tenuis*	×			×				×
16. *Phlebiella vaga*	×	×	×	×	×			×
17. *Stereum albobadium*	×	×	×	×	×	×	×	×
18. *Stereum crassum*	×		×		×	×	×	×
19. *Stereum complicatum*	×		×	×	×	×	×	×
20. *Stereum gausapatum*	×	×	×	×	×	×	×	
21. *Stereum ochraceo-flavum*	×		×	×	×		×	×
22. *Stereum ostrea*	×	×	×	×	×	×	×	×
23. *Stereum papyrinum*					×		×	×
24. *Stereum purpureum*	×	×	×	×	×		×	
25. *Stereum sulphuratum*					×		×	×
26. *Treichispora diademifera*	×	×	×	×	×	×	×	
27. *Xylobolus frustulatus*	×	×	×	×	×	×	×	

Tables I and II list the species we collected in Mexico and the regions in which they are reported to occur. Region VII should be considered to be completely filled, since this column represents the Mexican collections. However, those species for which we could find no previous report from Central America appear without checks in column VII. Table III records the percentages of species common in the various regions with our Mexican collections. Figures 1 and 2 are graphic representations of these percentages carried to the nearest whole number. Since these percentages are based only on Mexican collections, valid comparisons can only be made of Region VII with the other regions.

An inventory of Burt (1914-1926) and Murrill (1912) reveals that

TABLE II.—Distribution of certain Mexican Polyporaceae in North America

Species	Region							
	I	II	III	IV	V	VI	VII	VIII
1. *Bjerkandera adusta*	×	×	×	×	×	×	×	×
2. *Cerrenella ravenelii*					×			
3. *Coriolus abietinus*	×	×	×	×	×	×	×	×
4. *Coriolus maximus*					×		×	×
5. *Coriolus pinsitus*			×		×	×	×	×
6. *Coriolus sector*					×		×	×
7. *Coriolus versicolor*	×	×	×	×	×	×	×	×
8. *Cycloporellus iodinus*					×		×	×
9. *Daedalia elegans*			×		×	×	×	×
10. *Favolus rhipidium*			×	×	×			
11. *Fomes dependens*					×		×	×
12. *Fomes feei*					×		×	×
13. *Fomes geotropus*			×		×		×	×
14. *Fomes ohiensis*		×	×	×	×	×		×
15. *Fomes robiniae*	×		×	×	×	×	×	×
16. *Fomes roseus*	×	×		×		×	×	×
17. *Ganoderma lobatum*			×	×	×	×		
18. *Ganoderma lucidum*	×	×	×	×	×			
19. *Gloeophyllum sepiaria*	×	×	×	×	×	×	×	×
20. *Hapalopilus gilvus*	×	×	×	×	×	×	×	×
21. *Hapalopilus lichnoides*					×		×	×
22. *Hexagona tenuis*							×	×
23. *Irpex lacteus*	×	×	×	×	×	×	×	×
24. *Pogonomyces hydnoides*					×		×	×
25. *Polyporus arcularis*		×	×	×	×	×	×	×
26. *Polyporus biennis*	×	×	×	×	×			×
27. *Polyporus dichrous*	×	×	×	×	×	×		
28. *Polyporus occidentalis*							×	×
29. *Polyporus zonalis*					×		×	×
30. *Poria regularis*					×			×
31. *Poria taxicola*	×	×	×	×	×	×		
32. *Poria tenuis*	×	×	×	×	×	×		
33. *Pycnoporus sanguineus*		×	×	×	×	×	×	×
34. *Trametes rigida*			×	×	×		×	×
35. *Trametes sepium*	×	×	×	×	×	×	×	×

the sixty-two species considered here represent a substantial percentage of the known Mexican thelephores and polypores. Wherever possible, synonyms have been taken into account using the works of Boidin (1958; 1959a, b), Lowe (1957), Overholts (1953), Rogers and Jack-

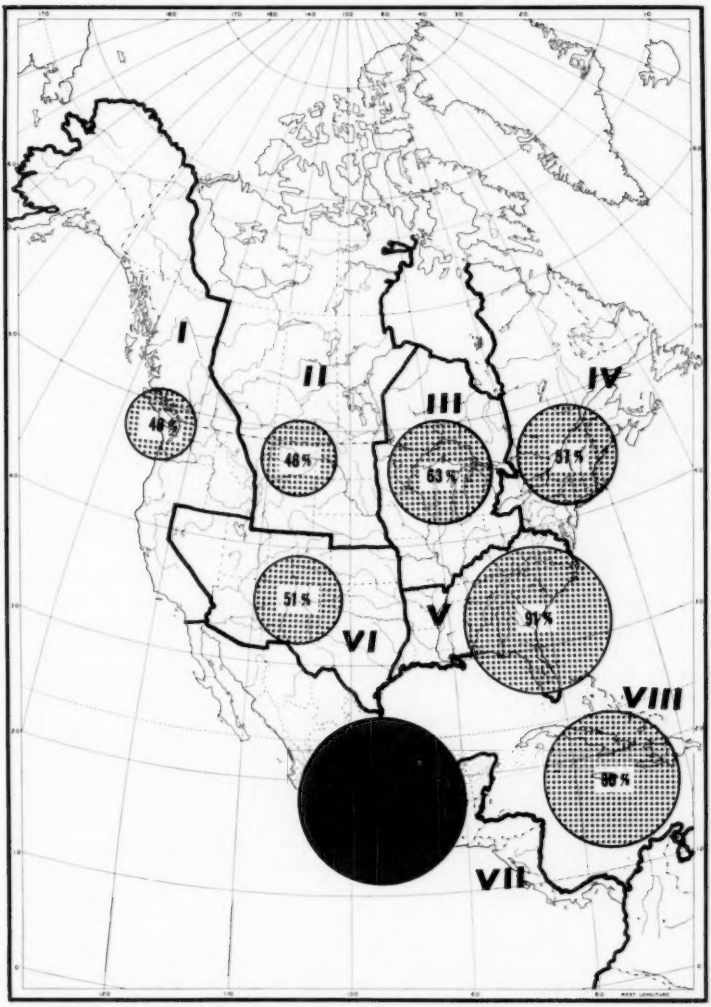

Fig. 2.—A comparison of the percentage of Mexican Polyporaceae (dark circle representing 100%) found in the remaining regions of North America. Based on a collection of 35 Mexican polypores, comparisons are valid only between Region VII and the other regions.

TABLE III.—Percentage of Mexican species represented in other regions of North America

Region	Thelephoraceae	Polyporaceae	Thelephoraceae and Polyporaceae
I	66.6	40.0	51.6
II	40.7	45.7	43.5
III	70.3	62.9	66.1
IV	62.9	57.1	54.8
V	85.2	91.4	88.7
VI	40.7	51.4	46.7
VIII	62.9	80.0	72.6

son (1943), and others. Accordingly, Burt lists seventy-two species from Mexico; to which we now add thirteen species not previously reported, bringing the total number to eighty-five species. Murrill gives one-hundred and eighteen species (twenty-four considered by him to be new to science); to which we add thirteen unreported by him, bringing the total number to one-hundred and thirty-one species. Therefore, our collection of twenty-seven thelephores and thirty-five polypores represents about 32 per cent of the known Mexican Thelephoraceae and 27 per cent of the Polyporaceae.

The most striking feature, in considering the Thelephoraceae (Fig. 1, Table III), is the high degree of identical species in Mexico and the southeastern United States. Sharp (1948) has shown a similar finding between the Mexican and Guatemalan highlands' fungi and the Appalachian fungi, using a number of species widely scattered in different taxonomic categories. Our collections were made from lowlands as well as highlands. Perhaps, this similarity could be enhanced by dividing the Mexican fungi into highland and lowland species and comparing them with the Gulf coastal plains and Appalachian species. The next highest degree of similarity is shown by comparing Region VIII and Region III. The Mississippi River basin appears to afford a favorable habitat for the thelephoraceous fungi which are also found in tropical and subtropical North America. Oddly enough, Pacific North America demonstrates a higher degree of similarity with Mexican Thelephoraceae than does the West Indies. This difference is not high and may be shown in the future to be caused by the lack of collecting in the Antilles. Regions II and VI show the poorest correlation. The lack of suitable substrates and abundant water may account for this. Finally, Region IV has a higher degree of similarity than Regions II and VI.

As in the Thelephoraceae, the Polyporaceae (Fig. 2, Table III) show the same correlation between Regions VII and V, with an even higher percentage of similitude. Region VIII, however, closely approaches Region V and here outranks Region III. The polypores are relatively well collected and this shift would not seem to be caused by better collecting in one area than another. This may well portend a similar shift in the thelephores as they become better known in Region

VIII. The relative paucity of polyporaceous species in common between Region VII and Region I, and the greater number represented in Regions II and VI is noteworthy. The Thelephoraceae seem to suggest the reverse with a larger percentage occurring in Region I. This difference cannot at present be explained. Once again, substrate relations might be considered.

Column 3 of Table III compiles the percentages of both Mexican thelephores and polypores as represented within the remaining regions. In decreasing order of similarity the Regions are V, VIII, IV, I, and II. Treating the families combined, however, is not as informative as keeping them separate. Indeed, comparisons at the generic level should prove to be even more interesting. It is also obvious that a world-wide comparison would be enlightening, but the lack of data at present makes this extremely difficult.

REFERENCES

BISBY, G. R. 1933. The distribution of fungi as compared with that of phanerogams. Am. J. Bot., **20**:246-254.

———. 1943. Geographic distribution of fungi. *Bot. Rev.*, **9**:466-482.

BOIDIN, J. 1958. Héterobasidiomycètes saprophytes et homobasidiomycètes resupinés: V.—Essai sur le genre *Stereum* Pers. ex S. F. Gray. *Rev. Mycol.*, **23**:318-346.

———. 1959a. Héterobasidiomycètes saprophytes et homobasidiomycètes resupinés: VI.—Essai sur le genre *Stereum* sensu lato. *Ibid.*, **24**:197-225.

———. 1959b. Héterobasidiomycètes saprophytes et homobasidiomycètes resupinés: VII.—Essai sur le genre "*Stereum* sensu lato." *Bull. Soc. Linn. Lyon*, **28**:205-222.

BURT, E. A. 1914-1926. The Thelephoraceae of North America. *Ann. Missouri Bot. Gard.*, **1**:185-228. 1914; **5**:177-203; 301-368. 1918; **7**:81-248. 1920; **12**:213-257. 1925. **13**:173-354. 1926.

GOODALL, G. and M. C. DARBY. 1953. *The University Atlas*. Geo Philip & Son, Ltd. London.

LANGE, J. K. 1934. Mycofloristic impressions of a European mycologist in America. *Mycologia*, **24**:1-70.

LOWE, J. L. 1957. Polyporaceae of North America. The genus *Fomes*. *Tech. Publ.* No. 80. N.Y. State Univ. College of Forestry at Syracuse Univ.

MURRILL, W. A. 1907. Polyporaceae. *North American Flora*, **9**(½):1-131.

———. 1912. The Polyporaceae of Mexico. *Bull. N.Y. Bot. Gard.*, **8**:137-153.

———. 1915. *Tropical Polypores*. Publ. by the author. New York.

OVERHOLTS, L. O. 1939. Geographical distribution of some American Polyporaceae. *Mycologia*, **31**:629-652.

———. 1953. The Polyporaceae of the United States, Alaska and Canada. *Univ. Mich. Stud. Sci. Ser.*, **19**:1-466.

REICHERT, I. 1921. Die Pilzflora Aegyptens. *Bot. Jahrbucher*, **56**:1-70.

ROGERS, D. P. and H. S. JACKSON. 1943. Notes on the synonymy of some North American Thelephoraceae and other resupinates. *Farlowia*, **1**:263-328.

SHARP, A. J. 1948. Some fungi common in the highlands of Mexico and Guatemala and eastern United States. *Mycologia*, **40**:499-502.

WELDEN, A. L. and P. A. LEMKE. 1960. Notes on Mexican fungi. *Bol. Soc. Bot. Mexico*, (in press).

Vocalization as an Isolating Mechanism in Frogs

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ABSTRACT: In laboratory tests, female *Hyla crucifer* selected the call of their own species in preference to that of *Pseudacris triseriata*, but not in preference to that of *P. ornata*.

Female *triseriata* selected the call of their own species instead of that of the allopatric leptodactylid *Eleutherodactylus portoricensis*. On the other hand, only about 8 out of 10 succeeded when given a chance to respond to the calls of sympatric hylids—*P. ornata*, *P. brachyphona* and *H. crucifer*. Local *P. triseriata* females were unable to discriminate between a call of a member of their own population and that of a frog recorded in New York; however, when given a chance to respond to a call recorded in Manitoba, 8 out of 9 reacted to the locally recorded call.

Thus, for some species, vocalization is a major isolating mechanism, for others it is partially effective, and for still others it is ineffective. In those species in which vocalization is not a complete isolating mechanism, other factors—such as body size, rather small and subtle differences in behavior, habitat preference and timing—prevent interspecific matings.

As is well known, optimum conditions for amphibian reproduction are generally associated with rainfall. At such times, numerous individuals of several species often aggregate in the same pond. In these situations, it is important that interspecific matings be avoided. The latter result in gross biological inefficiency. Special secretions produced by the hedonic glands of males contribute greatly in preventing interspecific matings from occurring among most caudate amphibians. Among the Anura, such glands are absent. Numerous workers (Noble, 1931; A. P. Blair, 1941a, 1942; W. F. Blair, 1955, 1956; and many others) have stated that the calls of anurans serve to prevent crossing of the various species utilizing the same breeding site. However, there are no experimental data to verify this conclusion. With the recent observations that *Pseudacris triseriata* undergoes reproductive behavior in the laboratory and that the mating call alone guides a female to a particular male (Martof and Thompson, 1958), a method was provided for the testing of frog calls as an isolating mechanism.

Acknowledgments.—This study was supported by the National Science Foundation. I am grateful to Paul Kellogg (Cornell University Library of Natural Sounds) for the use of recordings of *Pseudacris triseriata* made in New York and in Manitoba and for the recording of *P. ornata*. I am especially indebted to Eric F. Thompson, Jr. for the recording of *Eleutherodactylus*, for the preparation of the recorded calls used in this study, and for assistance with the tests.

Methods

From field-made recordings of various frogs (mostly sympatric hylids), single calls having a minimum of background noise were selected. Each call was transferred to a loop of tape constructed so that

the call was repeated at approximately its natural rate. In each test conducted, two such loops were simultaneously played back via the same type of recorders (Magnecord model Nos. P63 and P73) and and speakers (Mytron crystal earphones, model No. N-98). The speakers were placed at opposite ends of a 5′ x 8′ x4″ indoor tank, provided with numerous scattered clumps of sedges and grasses and with water having a uniform depth of about 0.75″. A 21-inch strip of burlap, supported by stakes placed every two feet around the tank, prevented frogs from jumping out of the tank. Furthermore, the burlap was an effective "screen" behind which observers could move without disturbing the frogs in the tank. Calls were played back with about the same relative loudness that they occur in nature. The more similar calls, those of various populations of *Pseudacris triseriata*, were adjusted by balancing the voltages across the speakers so that the intensity of each call was the same. After a few frogs were tested, the calls were shifted from one speaker to the other. Thus any bias in the tank or in the play-back systems tended to cancel out. This was done routinely even though such bias appeared to be absent.

Locally captured gravid females of *Hyla crucifer* and *Pseudacris triseriata* were used in this study. These are the only hylids which occur in Clarke County, Georgia and which breed in February and March. Practically all specimens were captured along highways near breeding areas. Only a few frogs were collected in the breeding areas. All specimens used in the laboratory were not in amplexus when captured. These animals were kept in a refrigerator at 6° C. and were used within a few days after capture. About an hour before the frogs were to be tested, they were placed in a sound-proof box where the temperature was the same as that in the laboratory (18-20° C.). The laboratory was evenly lighted by overhead fluorescent lights, dimmed during the tests. Each female was used once and at most, only two specimens were in the tank at the same time. The frogs to be tested were placed in a small screen enclosure located along one side of the tank midway between the speakers. Here they were retained for about 15 seconds — long enough to recover from handling, yet not long enough to evoke escape behavior due to confinement. Each female was observed closely and her path and behavior noted.

Upon release into the tank, most females remained motionless for several minutes. However, above a third of them went first into a nearby clump of vegetation before becoming quiescent. Only a few females reacted to a call immediately upon being released. Usually the first outward indication that a female was going to react was that she turned her head (often her entire body) and faced one of the speakers. Some frogs oriented toward one speaker and then toward the other — apparently they had some difficulty in making a choice. However, once a female began to show interest in the calls, a reaction soon followed. Usually she hopped directly

to a speaker and often upon it. When within a few inches in front of, or under, or on the speaker, she generally remained there 30 seconds to about 12 minutes. After responding to one call, some females responded to the call arising from the other speaker. This situation was further complicated because sometimes the second response was more intense than the first. Because of this type of behavior, two criteria were established as being prerequisite to a "reaction."

I. The frog had to move directly to a speaker and at the same time provide overt evidence that she was attentive to the call produced there. The latter consisted of (a) her facing the speaker, usually with head high and alert, and in the meantime (b) the absence of escape behavior (erratic hopping and much climbing onto the burlap around the tank). In every instance, there had to be no doubt that the frog got to a speaker by deliberate movements rather than by accidental wandering.

II. The second requirement for a "reaction" was that, had a male been present in place of the speaker, amplexus would have resulted as a consequence of the female's behavior. For each frog, only the first response which met these requirements was counted.

Depending on the amount and kind of activity shown by a female, an experiment was terminated if no reaction occurred within 30 to 60 minutes. Those females which did not respond to either call spent practically all their time in the vegetation where they remained quiescent or else they slowly climbed up the vegetation and eventually onto the burlap. Such behavior was identical to that of frogs not subjected to any calls. Accordingly, the number of these "non-reactions" was not considered in the determination of the probability associated with each set of experiments. Generally each series of tests included about ten reactions. The probability that the results (the ratio of the number of frogs which reacted to each call) were due solely to chance was determined by the Chi-square method.

RESULTS

Hyla crucifer

The results obtained for *Hyla crucifer* are more explicit than those for *P. triseriata*. The females reacted to the call of the male in a manner very similar to that described for *triseriata* (Martof and Thompson, 1958); however, the following differences were noted. The female *crucifer* spent more time on and in the vegetation, they hopped more, and climbed onto the speaker more. Furthermore, their average reaction time was 15.8 minutes which is shorter than that of *triseriata* (18.2 minutes). In both species about 88 per cent of the time spent in the tank involved a long pause which occurred immediately after a frog was released. Once a frog started to react, she usually went promptly to a speaker. There was one other way in which the behavior of *crucifer* was outstanding. After moving to a speaker, about a third of the females repeatedly jumped against the side of the tank near the speaker. They would hit into the tank wall

about three inches from the bottom and fall back into the water, often with venter up. One female did this 25 times within four minutes. This obviously was not escape behavior. *Hyla crucifer* is a graceful, agile hopper and climber, in sharp contrast these actions were definitely awkward, clumsylike. In *Pseudacris*, sex recognition usually involves the female's crawling into contact with the antero-ventral part of the calling male, whereas in *Hyla* the female usually jumps onto the male. Thus, the jumping against the side of the tank by the female *crucifer* very likely was a misdirected attempt to get to the sound source. This difficulty in localizing the sound was probably due to inherent qualities of the earphones used as speakers. Furthermore, male *crucifer* generally call from on vegetation a few inches to a few feet from the water; whereas, male *triseriata* call usually from in the water.

The call of *crucifer* is a short, clear, high-pitched whistle consisting of a single note with an upward slur at its end. This call has an average dominant frequency of 3200 cycles per second (cps) and a duration of 0.13 sec.; it is repeated about once per second. On the other hand, the call of local *triseriata* consists of a series of varied notes given in rapid succession so as to produce a penetrating, grating sound, often likened to that made by passing the thumb over the teeth of a comb. On the average, this pulsed call consists of 17 notes having a dominant frequency of about 2700 cps and a duration of 0.75 sec. It is repeated about every 2.5 sec.

All female *crucifer* used in 1959 were captured on March 11th. The next day some of them were given a choice of reacting to the call of their own species and to that of *triseriata*. Nine reacted to the call of *crucifer* and none to that of *triseriata* (Table I). The probability that such results would occur by chance alone is very slight

TABLE I.—The response of gravid female *Hyla crucifer* to a choice between a call of their own species and one of another species

Alternative	Number of females reacting to call of *crucifer* - alternative	Probability (Chi-square)	Efficiency of isolation (estimated)
Pseudacris triseriata (Athens, Ga.)			
Mar. 12, '59	9 - 0		
Feb. 24, '60	14 - 1		
total	23 - 1	.001	92%
Pseudacris ornata (Gainesville, Fla.)			
Mar. 12 & 15, '59	10 - 11		
Feb. 29, 1960	13 - 7		
total	23 - 18	.60	8%

(0.03). Obviously, female *crucifer* are effectively isolated from male *triseriata*.

On the same night, some *crucifer* females were subjected to the call of their own species and to that of *Pseudacris ornata*. The call of *ornata* consists of a single note which is also loud and distinctive; however, it is only about one-fourth as long as that of *crucifer* and is repeated about twice as frequently. It has an average dominant frequency of 2800 cps and is more metallic in quality (suggesting the sound made by a hammer squarely hitting a chisel).

In sharp contrast to the results obtained with the *triseriata* call, the female *crucifer* showed no preference for the call of their own species over that of *ornata*. Three females selected the call of *crucifer* while four responded to that of *ornata*. Three days later, more females were tested. At this date, seven females reacted to each call making a total of 10 reactions to the call of *crucifer* and 11 to that of *ornata*. The probability that selection of the call was due to chance alone is very high. Accordingly these data strongly suggest that the frogs were unable to discriminate between the calls offered. This is of great biological importance because about 90 per cent of the geographic range of *ornata* is also occupied by *crucifer*.

In 1960 additional observations were made. On February 24th, *crucifer* females captured in the field only a few hours previously were subjected to *crucifer* and *triseriata* calls. Fourteen of the 15 which reacted went to the call of their own species. The single reaction to the *triseriata* call was in every way similar to those made to the call of *crucifer*. Moreover, the frog involved was morphologi-

TABLE II.—The response of female *Pseudacris triseriata* to a choice between a call of the same population and one of another population

Alternative	Number of females reacting to call of *triseriata* - alternative	Probability (Chi-square)	Estimated Efficiency of isolation
P. triseriata (Rochester, N. Y.)			
Feb. 26, '59	5 - 5	1.00	0%
P. triseriata (Ft. Churchill, Man.)			
Feb. 24, '59	8 - 1	.10	78%
P. brachyphona (Amicolola Falls, Ga.)			
Feb. 27, '59	9 - 3	.22	50%
P. ornata (Gainesville, Fla.)			
Mar. 1, '59	8 - 2	.20	60%
Hyla crucifer (Athens, Ga.)			
Mar. 14, '59	8 - 2		
Feb. 10, '60	7 - 2		
total	15 - 4	.08	58%
Eleutherodactylus sp. (Puerto Rico)			
Feb. 28, '59	3 - 0	.22	100%

cally a *crucifer*. This is significant because hybrids of these two species have been produced in the laboratory (Blair, 1941b, Gosner, 1956). The over-all performance of 23 reactions to the call of their own species and only one to that of *triseriata* indicates that a high degree of isolation is afforded by vocalization.

On February 29th, freshly captured *crucifer* were tested against the call of *ornata*. Thirteen of the 20 reactions were to the call of *crucifer*. These results are in general consistent with those obtained in 1959 and indicate a relatively low degree of vocal isolation.

Pseudacris triseriata

Between February 24 and March 14, 1959, 54 female *triseriata* reacted to a choice between the call of a local *triseriata* and that of another population. Calls from specimens recorded in New York and Manitoba closely approximate that of local specimens (Thompson and Martof, 1957). However, the Manitoba call has the highest dominant frequency (3100 cps) and the shortest duration (0.58 sec.). These characteristics make it less melodic and more tinny in quality. On the other hand, the call of *triseriata* from New York is very similar to that of local frogs in average dominant frequency (2600 cps) but is more like the Manitoba call in duration (0.60 sec.). The call of the New York population has 20 notes, that from Manitoba 18 notes.

In this series of tests, a surprisingly large number (five out of ten) of the local females was attracted to the New York call. In sharp contrast, only one female out of nine preferred the Manitoba call to that of the local population. The latter results are significant at the ten per cent level of probability and possibly indicate some isolation.

The calls produced by other species of *Pseudacris* (*brachyphona* and *ornata*) were also tested. Because of its nasal quality the call of *brachyphona* is easily distinguished (by humans) from those of the various populations of *triseriata*. Its call is of shorter duration (0.46 sec.), has a lower average dominant frequency (2250 cps), and contains many more notes (about 25). Three of the twelve female *triseriata* tested, selected the call of *brachyphona* to that of *triseriata*. The probability that these results were due to chance alone is 0.22.

Even though the call of *ornata* is very different from that of *triseriata*, two of the ten female *triseriata* tested, preferred it to that of their own species. These results are significant at the six per cent level of probability.

As described earlier, the call of *ornata* is similar in many of its parameters to that of *crucifer;* furthermore, female *crucifer* reacted equally well to the call of *ornata* and to that of their own species. Accordingly, it is of special interest to note that two out of ten *triseriata* selected the call of *crucifer* to that of *triseriata*. This is the same ratio as was obtained when the call of *ornata* was used.

In contrast to the previous experiments with sympatric and closely related forms, the call of the allopatric, *Eleutherodactylus portoricensis* was used. The common name of this frog, "co-qui," very adequately describes its call which consists of two distinct notes of equal duration (0.091 sec.). These notes are separated by a relatively long interval (0.137 sec.) and differ greatly in their average dominant frequencies, 900 and 2050 cps, respectively. When three female *triseriata* were given a choice between this call and that of their own population, they reacted to the latter. In as much as they showed no interest in the call of *Eleutherodactylus*, additional specimens were not tested.

In 1960 *triseriata* were again tested with a call of a local *triseriata* and one of *crucifer*. Seven of the nine females which reacted went to the call of their own species. These data are in accord with those obtained in 1959.

DISCUSSION

It is recognized that the absence of a background chorus of calling frogs produced a somewhat artificial setting for the testing of frogs; however, in a study of a complex stimulus, such as the mating call, it is highly desirable to isolate the call so that it can be subjected to more careful scrutiny. Moreover, the results obtained indicate that background calls are not essential to the reaction of the female; however, had they been present, it is possible that the frogs would have reacted more quickly. Other artificialities included changes in the acoustic properties of the environment, differences in lighting, small changes incidental to recording and playback of calls, etc. Temperature differences were also involved. For example, the call of local *triseriata* was recorded at a temperature of 15.0° C. (water), *crucifer* at 17.8° (air), *Eleutherodactylus* at 29.4° (air), and *brachyphona* at 8.9° (water). For the other calls, temperature data were not available. Also lacking were details on recording conditions, such as location of microphone with regard to the calling frog. In spite of the absence of these desiderata, the general characteristics of the calls of each species are contained rather accurately in the test calls.

Why all frogs did not react is difficult to determine. Many factors are here involved: mainly, individual differences in their internal state of readiness for reproduction and secondly, differences in their adjustment to handling and to laboratory conditions. Also to be mentioned, is the possible effect of refrigeration. Table III contains a list of the number of frogs that did not react in each series of tests and also the duration of the periods of refrigeration. No clear-cut relationship is evident. In 1960 the *triseriata* were dissected immediately upon being tested. It is highly pertinent that the eggs of the nine females that reacted were in the ovisacs while those of the three that did not react were still in the ovaries. These data strongly suggest that ovulation is prerequisite to mating for this species.

Because of the relatively small number of animals used in this study, the results for each set of tests provide only a general approxi-

mation of the degree of isolation afforded by vocalization. The general efficiency of each set of calls was determined in the following way. If as many females went to one call as went to the alternative, the efficiency was interpreted to be 0 per cent. Likewise, if all females reacted to the call of their own species, the efficiency was 100 per cent. Accordingly, if three out of ten went to the alternative call, the efficiency was only 40 per cent. The efficiency of the various sets of calls is provided in Tables I and II. For some groups, such as female *crucifer* and male *triseriata*, vocalization is a highly effective isolating mechanism. In contrast, female *triseriata* are not completely isolated by vocalization from any of the other hylids tested.

The amount of isolation between two species is not completely dependent upon the amount of structural differentiation exhibited in their calls. This is clearly indicated by the fact that *triseriata* females responded to most calls made available to them. These calls varied considerably in complexity, yet about the same proportion of females reacted to each (see Table II). Structural differentiation of calls may produce isolation but some major physical changes seemingly do not alter the isolative powers of calls.

It is imperative that the differential effectiveness of calls be considered for all species wherein reproductive isolation is studied. For example, four out of 19 female *triseriata* responded to the call of *crucifer;* however, only one out of 24 female *crucifer* responded to the call of *triseriata*. Because of the greater efficacy of vocalization in the reciprocal mating, the efficiency of isolation between these species is not 58 per cent (as given in Table II) but more accurately is 75 per cent. Because reciprocal tests for the other groups are not currently available, the data in Tables I and II are based on unilateral experiments.

TABLE III.—The temporal distribution of "non-reactions" and their relationship to refrigeration

Date	Days under refrigeration	Number of Reactions - Non-reactions	Percent which did not react
Hyla crucifer			
Mar. 12, '59	1	16 - 2	11
Mar. 15, '59	4	14 - 4	22
Feb. 24, '60	0	15 - 2	12
Feb. 29, '60	0	20 - 3	13
Pseudacris triseriata			
Feb. 24, '59	10	9 - 2	18
Feb. 26, '59	0	10 - 4	29
Feb. 27, '59	1	12 - 2	14
Feb. 28, '59	2	3 - 0	0
Mar. 1, '59	3	10 - 2	17
Mar. 14, '59	3	10 - 1	9
Feb. 10, '60	0	9 - 3	25

Another factor which must be considered, if reproduction isolation is to be evaluated precisely, is the relative sizes of the populations occupying a particular breeding area. This is especially applicable to local *crucifer* and *triseriata*. The main part of the *triseriata* population breeds somewhat earlier in the season than does the main part of the *crucifer* population. As a consequence, *crucifer* males are relatively scarce during the peak of the *triseriata* breeding season and *triseriata* males are less abundant during the peak of the *crucifer* season. There is yet another factor which is pertinent. The calling *triseriata* males are usually more closely aggregated than are those of *crucifer*, even during the peak of the latter's breeding season. Thus interspecific matings between these sympatric forms are greatly inhibited by many factors, none of which is completely successful when operating alone.

It is noteworthy that *triseriata* having a relatively elaborate call, is not completely isolated from most related species — those with equally elaborate calls as well as those with simpler calls. In contrast, *crucifer* has a relatively simple call and is effectively isolated from *triseriata* (and very probably from others with similar calls) but not from *ornata*, which also has a simple call.

This study provides a method wherein the effectiveness of vocalization as an isolating mechanism can be accurately measured for many species. However, what is critically needed to promote understanding of the role of vocalization is knowledge of (1) those parameters of a call which elicit a reaction from a female frog, and (2) the hearing ability of frogs.

REFERENCES

BLAIR, A. P. 1941a. Variation, isolation mechanism and hybridization in certain toads. *Genetics*, **26**:398-417.

———. 1941b. Isolating mechanisms in tree frogs. *Proc. Nat. Acad. Sci.* **27**:14-17.

———. 1942. Isolating mechanism in a complex of four species of toads. *Biol. Symposia*, **6**:235-249.

BLAIR, W. F. 1955. Mating call and stage of speciation in the *Microhyla olivacea* — *M. carolinensis* complex. *Evolution*, **9**:469-480.

———. 1956. Call differences as an isolating mechanism in southwestern toads (genus *Bufo*). *Texas J. Sci.*, **8**:87-106.

GOSNER, K. L. 1956. Experimental hybridization between two North American tree frogs. *Herpetologica*, **12**:285-289.

MARTOF, B. S. AND E. F. THOMPSON, JR. 1958. Reproductive behavior of the chorus frog, *Pseudacris nigrita*. *Behavior*, **13**:243-258.

NOBLE, G. K. 1931. *The Biology of the Amphibia*. McGraw-Hill Book Co., New York.

THOMPSON, E. F., JR. AND B. S. MARTOF. 1957. A comparison of the physical characteristics of frog calls (*Pseudacris*). *Physiol. Zool.*, **30**:328-341.

Observations of the Activities of Small Animals (Reptilia and Mammalia) on a Quadrat in Southwest Texas

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ABSTRACT: Observations on the daily activities of reptiles and small mammals were made on a quadrat near Alpine, Brewster County, Texas, during the early summer of 1957. Thirty-six live-mouse traps and nine nest boxes were arranged in grid patterns on a quadrat 300 feet square. Thirteen drift-fence traps were arranged in two lines which bisected the quardrat in north-south and east-west directions, and crossed in the center of the quadrat.

During the study 114 reptiles of nine species, mostly lizards, were marked and released, and 74 of these were recovered at least once for a total of 230 recoveries. Whiptail lizards (*Cnemidophorus sacki*) formed the bulk of the reptiles captured and recovered. Nineteen mammals of three species were marked and released, and seven were recovered for a total of 22 recoveries. On the basis of the observed activities of other animals reported in various papers, it is proposed that the term "home realm" be adopted for all of the area in which an animal is normally active. The term "home range" then becomes restricted to the smaller, inner area in which an animal is usually active.

In recent years, there have been a number of investigations of the population dynamics of reptiles and mammals in southwestern Texas. York (1949) studied the movements of mice in the Sierra Vieja range of Presido county, and Anderson (1949) recorded the activities of mule deer in the same area. Louis Follansbee (1951, unpublished) and Dixon (1958) studied the movements of mice on the Black Gap Wildlife Management Area of Brewster county. Milstead (1957 a,b,; 1959; In press) compared the activities of *Cnemidophorus* and other lizards at Black Gap and other stations, and W. G. Degenhardt is currently completing an investigation of the movements of various reptiles in Big Bend National Park. The present report is concerned with another study of population dynamics of small vertebrates in southwest Texas, but this work differs from the others in that it was the first attempt to study reptiles and mammals simultaneously on the same quadrat. In effect, it was an attempt to study the movements of all small vertebrates exclusive of birds. The purpose of this paper is to report on the methods used, the effectiveness of those methods, and the observations made.

The study area is located on the Sul Ross State College Ranch, one mile east of Alpine, Brewster County, Texas. The work was done by a Sul Ross field zoology class under the direction of the writer from June 6 to July 9, 1957.

Acknowledgments.—Thanks are due the members of the Department of Range Animal Husbandry for permission to carry out this study on land in their

charge. I am indebted to Dr. Barton H. Warnock of the Sul Ross Biology Department for information on the vegetation of the region. Special credit is due the fourteen field zoology students who in their study of ecology in the field made the bulk of the observations here reported. Especial thanks are accorded Mr. Reece DeGraffenried for his aid in preparation for the course.

STUDY AREA

The Sul Ross State College Ranch lies in the eastern portion of the Davis Mountains biotic district of Blair (1940, 1950) and Milstead (In press). The study area exhibits no outstanding faunistic or floristic differences from the interior of the district. The Davis Mountains are in the Chihuahuan biotic province of Blair (1940, 1950) and Dice (1943), and in the Basin and Ranges physiographic province of King (1937). The quadrat was located in the Short-Grass—Mesquite association of Blair (1940). The dominant vegetation of the quadrat consists of low mesquite (*Prosopis juliflora*), mescat (*Acacia constricta*), lote bush (*Condalia lycioides*), tasajillo (*Opuntia leptocaulis*), prickly pear (*Opuntia sp.*) yucca (*Yucca torreyi* and *Y. elata*), and local stands of grasses, tobosa (*Hilaria mutica*), blue grama (*Bouteloua gracilis*), and black grama (*Bouteloua eriopoda*). The average elevation of the quadrat area is about 4600 feet. Except for a slight rise in the northwest corner and a slight, over-all dip to the east, the site of the quadrat is fairly level. Drainage is into a small draw located about 50 yards to the east of the study area.

METHODS

The quadrat was 300 feet square and three types of traps were employed on it: 36 live-mouse traps built according to the specifications given by Blair (1941), nine nest-box traps similar to those used by Howard (1949), and 13 drift-fence traps of the type used by Milstead (1957b, 1959). The live-mouse traps were arranged in a grid pattern with approximately 60 feet separating the traps. The distances between the traps were not always exactly 60 feet, but varied as much as 10 feet from this figure in order to better utilize available natural cover. The outer lines of the live-mouse traps formed the boundaries of the quadrat. The nest boxes were arranged in a smaller grid within the mouse trap grid. The nest boxes were separated by approximately 125 feet, and distances of approximately 40 feet separated the boxes and the mouse traps. The drift-fence traps were spaced 50 feet apart and were connected by 12-inch-high drift fences. The traps and fences were arranged in the pattern of a cross with one line bisecting the quadrat from north to south and the other from east to west. The center trap where the two lines crossed was constructed in the shape of a cross with an entrance facing each direction. The approximate positions of all of the traps and fences are shown in Figure 1.

During the first few days of the study and on the last day, all of the students and the writer were present on the quadrat. For most of the

study, however, no more than eight people were on the quadrat at any one time.

The 36 live-mouse traps were baited on all but three nights of the study for a total of 1,008 trap nights. The bait consisted of a mixture of rolled oats and peanut butter. Although both the traps and the bait had been used previously in the same area with success, there were few captures and recoveries during this study. Simultaneous use of this type of trap and bait by the same workers at various other localities throughout the Davis Mountains also yielded poor returns. This suggests that the poor results may have been due to low rodent population density during the summer of 1957. The traps on the quadrat were closed during the daytime to prevent lizards from entering, tripping the trigger, and then perishing from the heat which accumulates in the traps during the day. The closure of the traps also prevented the entrance of ground squirrels (*Citellus*) and other diurnal animals. This was the only outstanding disadvantage of working with reptiles and mammals simultaneously.

The nest boxes were buried in the ground with only the lids and entrances protruding. They were not baited, but were provided with newspapers for nesting material. During the study, only one animal, a lizard (*Cnemidophorus sacki*) was found in a nest box. Although the boxes were left in the ground and periodically checked until late November, no small animal ever used them for a nesting site. The apparent low rodent density in 1957 may explain the failure of these traps. Workers in other parts of Texas (Blair, 1958; Blair and Kennerly, 1959; McCarley, 1958), however, have reported that rodents are reluctant to use nest boxes during the summer months. The boxes on the quadrat were eventually rendered useless by influx of silt and debris during floods created by fall rains. During use of nest boxes in overgrazed, arid regions, where rapid water run-off occurs, it is suggested that the entrances to the boxes project at least two inches above ground.

The drift-fence traps were operated with dirt-covered entrances, with overhanging shades, and without trapdoors, as described by Milstead (1957b, 1959). The traps were not baited, although trapped animals may have served to some extent as bait for other animals. For the most part, however, captures were the result of animals having been guided into the traps by the drift fences. The traps and fences were kept in continuous operation for the first week of the study and proved to be highly effective with lizards. After the first week, the number of captures and recoveries showed a marked decline. Apparently, the effectiveness of the traps and the number (15) of people on the quadrat during the first few days of the study caused the lizards to avoid the traps and fences. The traps were removed on the eighth day of the study. They were replaced on the 12th day and the number of captures and recoveries showed a slight increase for the next few days. For the remainder of the study, the traps were kept in operation for only four consecutive days of each week. In spite of these difficul-

ties, the number of captures and recoveries indicates that this crossed-lines method of drift-fence trap operation is better than the standard single-line method. It is suggested for future studies, however, that better data may be obtained if the traps are used on alternate days or kept in operation for no more than two consecutive days. In addition to lizards, two snakes (*Masticophis* and *Hypsiglena*), two pocket mice (*Perognathus*), and various invertebrates were captured in the drift-fence traps.

After capture, mice and lizards were permanently marked by toe clipping. The toes were so numbered that no more than one toe was removed from any one foot. One snake was marked by clipped subcaudal scales, and a turtle by a notch cut in the first marginal scute. Two jackrabbits were marked with ear notches. In addition to permanent marking, lizards were temporarily marked with a bright lacquer which permitted easy recognition until ecdysis or abrasion removed the lacquer (see Milstead, 1959, for a discussion of this marking method). Recoveries of these lizards and other animals outside of traps were recorded in number of paces to the nearest trap or nest box.

WEATHER AND ANIMAL ACTIVITY

A weather station was maintained in the center of the quadrat throughout the study. The instruments included a maximum-minimum thermometer for air temperatures, a modified Mason's form hygrometer, a portable anemometer with a recording needle for maximum wind gusts, and a clear-bulb thermometer for reading soil temperatures. The maximum-minimum thermometer and the hygrometer were mounted in a weather box four feet above the ground and the anemometer was attached to the exterior of the box. Soil temperature was taken with the full length of the thermometer bulb stuck into the soil and the remainder of the thermometer shaded from direct sunlight. The Mason's form hygrometer was modified by the substitution of a wet-bulb, Schultheis museum thermometer for the standard wet-bulb thermometer. This permitted more rapid readings, and readings that compared more favorably with a sling psychrometer.

The average minimum air temperature during the study was 18.5° C., and the average maximum was 34.4° C. The lowest temperature recorded was 13.0° C. on June 20, and the highest was 41.0° C. on June 28. The highest soil temperature recorded was 55° C. on several days at intervals throughout the study. The highest wind velocity recorded was 40 km/hr on the morning of June 11 before lizard activity began. The highest recorded during lizard activity was 30 km/hr. Wind appeared to have little influence on the trapping of mammals or on reptile activity. No sustained winds of high velocity were recorded during the study, however. Use of the anemometer was discontinued after the second week upon failure of a bearing. Rain fell on four occasions during the study, but amounted to less than half an inch each time. Each rain was a cloudburst of short duration.

In Table I, averages of relative humidity and soil and air tempera-

tures are given for each hour of the morning, and the total numbers of reptile records are given for each half hour. Time is used here as the only available standard for comparison. The relative humidity and temperatures of any given moment are dependent upon a number of factors, but they do show a diurnal trend. This trend is evidenced by comparing the hourly averages. Reptile activity follows the same trend as the relative humidity and soil and air temperatures, but is most closely correlated with soil temperature (Table I and Milstead 1957b, 1959). The average temperatures of the Alpine area are considerably lower than those given by Milstead (1959) for the Black Gap area in southern Brewster county. This is attributed to differences in elevation. The Alpine area is approximately 2,000 feet higher than Black Gap. As a possible response to the lower temperature of Alpine, the lizards have a maximum activity period of about half that of Black Gap lizards: 9:00 to 10:30 AM at Alpine and 8:00 to 11:00 AM at Black Gap. For the most part, however, the species and subspecies differ at the two areas, and this may be the reason for the activity differences.

Most of the mammal captures were in traps. The traps were checked at approximately the same time each morning, and there is no way of determining at what hour or temperature a trap was entered. Of a total of 39 captures of *Perognathus hispidus* and *Dipodomys merriami*, 26 were made during the seven days from June 25 to July 1. These were the hottest days and nights of the study, but also the time during which the moon was in its darkest phases.

HOME RANGE, TERRITORY AND HOME REALM

Many terms have been used to describe the areas within which animals move about as they carry out the normal functions of their lives. Only two terms, however, "home range" and "territory," have

TABLE I.—Correlation of total reptile records, average soil and air temperatures, and average relative humidity with morning time intervals (see text for further explanation).

	Time							
	0800	0830	0900	0930	1000	1030	1100	1130
Species								
Terrapene ornata	1							
Holbrookia maculata	4	9	7	9	8	7	2	
Sceloporus undulatus	4	3	2	3	2	3	1	
Phrynosoma modestum	1	2		1	2	2	1	
Cnemidophorus sacki	14	15	31	27	39	36	22	2
Masticophis flagellum					1			
Total Reptiles	24	29	40	40	53	48	27	2
Soil temperature °C.	26.6		30.8		37.2		41.9	
Air temperature °C.	24.7		26.4		28.0		29.4	
Relative humidity %	57.3		48.5		42.4		40.5	

received general acceptance. Burt (1943, p.351) concisely defines these terms: "Home range then is the area, usually around a home site, over which the animal normally travels in search of food. Territory is the protected part of the home range, be it the entire home range or only the nest." Adequate summaries of other terms used and of animals studied up to 1943 may be found in the papers of Nice (1941), Stickel and Cope (1943), and Burt (1943). The vast amounts of data summarized in these papers and presented in later papers indicate that most, if not all, terrestrial vertebrates demonstrate some form of home range behavior, and many exhibit territoriality. The data also indicate that most animals with definite home ranges make occasional trips outside of them for reasons which are usually undetermined. In calculating home range size, some workers include all of the area within which a given animal is captured, while others delete the area that is only visited occasionally. The definition given by Burt (and others) does not help to resolve the problem. If most animals periodically stray outside of the area in which they are most active, then the wanderings are normal activities and the area covered might be considered as part of the home range. These wanderings frequently appear to be at random with respect to direction and distance, and if included as a part of the home range would devalue the use of home range calculations in comparing animal activities. It is here proposed, therefore, that another term, "home realm," be adopted to include all of the area within which an animal is normally active from day to day. The term "home range" then becomes applicable only to the smaller area in which an animal is *usually* active. The term "territory" remains applicable to the part defended and may be less than, equal to, or greater than the home range, but would not be expected to be greater than the home realm. Thus, the larger area shown for the *Holbrookia maculata* in Figure 1 is the home realm and the smaller area within it is the home range.

ACCOUNT OF SPECIES

Altogether, 133 individuals of 12 species of reptiles and mammals were captured, marked, and released. Of these, 81 were recovered at least once for a total of 252 recoveries. The percentage of the total number of animals marked during each of the five weeks of study was as follows: (1) 66.4%, (2) 9.1%, (3) 15.2%, (4) 5.3%, and (5) 3.3%. One mouse was marked on the last day of study which was the first day of the sixth week.

The maximum number of recoveries for any single animal was 21 for a female *Holbrookia maculata*. Home ranges and realms were calculated for any animal with more than five records (initial capture plus recoveries), except where the records tended to fall along a single, straight line. The records of 11 lizards and one mouse exceeded the arbitrary restrictions. Their home ranges and realms were plotted by marking their points of record on graph paper, joining the outermost points with ruled lines, and calculating the square feet in the enclosed

area. Although, it is highly improbable that any animal moves about in straight lines, this method does provide some estimation of the area covered by an animal in its movements, and a means of comparing areas.

REPTILIA

A total of 114 reptiles of nine species was captured, marked, and released during the study. These consisted of one turtle, 112 lizards of seven species, and one snake. One other snake (*Hypsiglena torquata ochrorhyncha*) was captured in a drift-fence trap, but it was preserved rather than released. The turtle (*Terrapene ornata*), and the one snake (*Masticophis flagellum testaceous*) released, were not recovered. Individuals of three of the lizard species were not recaptured. These included a single greater earless lizard (*Holbrookia texana*), a male and female horned lizard (*Phrynosoma cornutum*), and a single Great Plains skink (*Eumeces obsoletus*). Of the remaining 108 lizards captured and released, 74 were recovered at least once for a total of 230 recoveries.

Holbrookia maculata approximans Baird. Speckled Earless Lizard. Nine females and seven males of this species were marked. Six females and all of the males were recovered at least once for a total of 48 recoveries. There were 22 records for one female, five for another, and nine for one male. The home range of the female with 22 records equalled 0.181 acre and the home realm equalled 0.628 acre (Fig. 1). The home range of the male was 0.169 acre. The area in which the other female was recorded was 0.349 acre and this possibly included part of the home realm other than the home range. The three home ranges, although all within the quadrat, showed very little overlap. This and the low numbers of this species marked on the quadrat suggest territorial habits.

The nine females varied in length from 50 to 55 mm, average, 52.0 mm; the seven males varied from 54 to 61 mm, average, 56.8 mm.

Sceloporus undulatus consobrinus Baird and Girard. Southern Prairie Lizard. Three females and four males of this species were marked. All were recovered at least once for a total of 22 recoveries. There were six records for one female and nine for a male. The home ranges were calculated at 0.139 acre for the female and 0.132 acre for the male. Body length in the three females varied from 59 to 62 mm; that of the males, from 55 to 63 mm, with an average of 58.0 mm.

Phrynosoma modestum Girard. Round-tailed Horned Lizard. One female and five males of this species were marked and released. Two of the males were recaptured once and the female was recaptured twice. The female was 45 mm in length, and the length of the males varied from 50 to 56 mm with an average of 54.0 mm.

Cnemidophorus sacki. A total of 79 whiptail lizards, 47 females and 32 males, was marked and released over the five weeks of the study. Of these, 51 were recovered at least once for a total of 156 recoveries. Seven whiptails were recovered more than five times and

their activity areas were mapped. The records of two of these proved to be along a trap line and were discarded. Two of the remaining five lizards were recaptured 13 times (the home range of one is shown in Figure 1); one, 11 times; one, eight times; and one, seven times. The minimum home range was calculated at 0.25 acre, the maximum at 0.43 acre, and the average at 0.34 acre. The lizard with the maximum area was recovered one time outside its home range. Addition of this

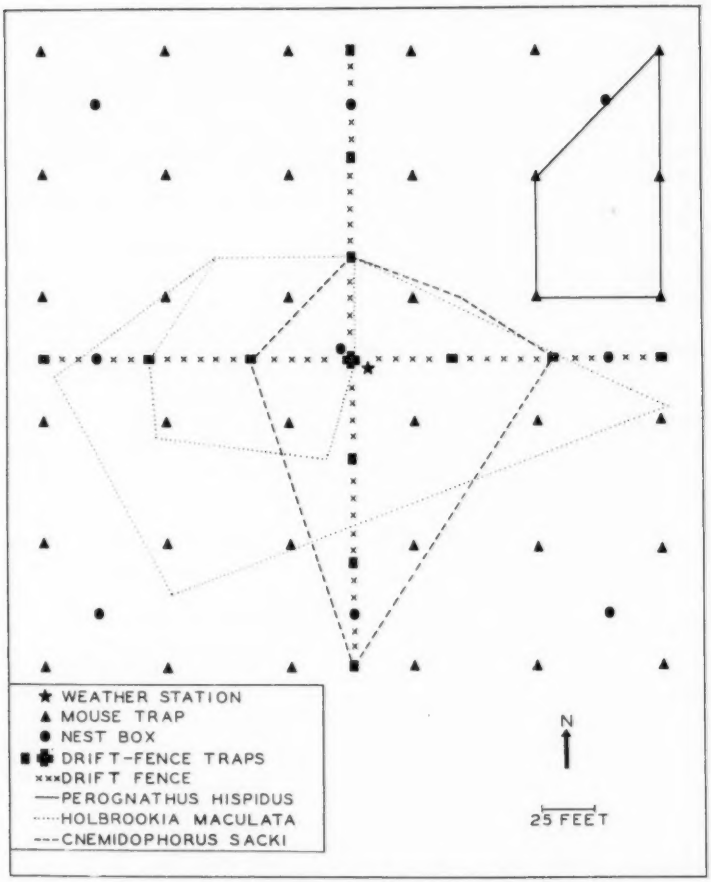

Fig. 1.—Diagram of quadrat lay-out on the Sul Ross State College Ranch during the 1957 summer and of the activity areas of three of the animals studied. The small inner area shown for *Holbrookia maculata* is the home range and the larger area is the home realm. Further explanation of the figure is given in the text.

point to a map of the lizard's movements yields a home realm of 0.76 acre. Milstead (1957b) calculated the home range of an individual of *Cnemidophorus tigris* at Black Gap at 0.26 acre and its home realm at 0.53 acre. When the figures for the home range and the home realm of the Alpine *C. sacki* are compared with those for the Black Gap *C. tigris*, it is found that the figures agree fairly well, proportionally (26/53: 43/87). The home range areas calculated for the two species also compare favorably with the home range areas calculated for *Cnemidophorus sexlineatus* in Kansas by Fitch (1958).

Milstead (1957b) found that the home ranges of several individuals of *C. tigris* showed considerable overlap. This, and the failure of the lizards to patrol their home ranges, was taken as an indication of lack of territoriality. The same observations hold true for *C. sacki* at Alpine.

Fitch (1958) calculated the population density of *C. sexlineatus* in Kansas to have been 65 per acre in 1953, 40 in 1954, 49 in 1955, and 72 in 1956. The 79 individuals of *C. sacki* marked on the Alpine quadrat give a figure of approximately 38 per acre. A Lincoln Index estimation based on the captures and recoveries of the first two days of the study gives a slightly lower figure: 72 lizards total, or 35 per acre. In arriving at these figures by means of a Lincoln Index, the first day (June 6) is used as the precensus period and the second day as the census period. Thus, A/B : C/D = 24/B: 8/16; B = 24 × 16/8 = 48. Lincoln Index = A + B = 24 + 48 = 72. The symbol "A" represents the number of lizards marked on June 6, "B" the number unmarked on June 6, "C" the number marked on June 6 recaptured on June 7, and "D" the number of unmarked lizards captured on June 7.

Only 51 of the 79 marked lizards were ever recaptured. If it is presumed that transients captured once will not be captured again, that residents will be recaptured at least once, and that the number of recaptures of any individual will be directly proportional to the amount of its home realm lying within the trapping area, then it may be assumed that approximately 51 of the marked lizards were residents and 27 were transients involved in either migration or exploration. A figure of 42 residents is obtained by modifying the Lincoln Index on the basis of the above presumptions. Thus, A — E/B: C/D — F = 24 — 3/B: 8/16 — 8; B = 21 × 8/8 = 21. Modified Index = A — E + B = 24 — 3 + 21 = 42. Symbols A through D are the same as above. Symbol "E" is the number of lizards marked on June 6 never recovered, and "F" is the number marked on June 7 never recovered. The number of lizards with at least a part of their home realm in the quadrat area may be presumed to be between 42 and 51, or between 20 and 25 resident lizards per acre.

Deaths of six marked lizards were recorded during the study. Three died of overheating in mouse traps, one was swallowed by a snake (*Hypsiglena*) in a drift-fence trap, one was partially eaten by an unknown predator, and one died of unknown causes.

Female *C. sacki* varied from 45 mm to 95 mm in length, average, 66 mm; males, from 55 mm to 88 mm, average, 70.7 mm. No definite size groupings were indicated in the measurements. Fitch (1958) found that young whiptails grow rapidly before and after their first hibernation and reach adult size by the end of their first year. Rapidity of growth decreases with increasing size. Thus, by June or July there is very little size difference between the age groups of yearling lizards and the adults of two or more years.

Observations of the foods and feeding habits of the Alpine *C. sacki* agree in general with those recorded for this species by Milstead (1957a). During the study, whiptails were observed to feed on scorpions (Scorpionida), grasshoppers (Acrididae), termites (Amitermes), candleflies (Lepidoptera), lepidopteran larvae, and ant lions (Myrmelionidae). Several students attempted to follow whiptails in their daily movements and concluded that the lizards travel in small, irregular circles about 20 feet in diameter during foraging. The whiptails appeared to continuously forage in the same general area every day, but within this general area they changed the site of the foraging circle every few days. One whiptail was seen to leap into the air and seize a flying oil beetle (Meloidae) which it later abandoned because of inability to kill the insect, or because of the oil secretion. On one occasion, two whiptails were observed in a drift-fence trap along with a sun spider (Solpugidae). The lizards ignored the arachnid in their efforts to escape from the trap, but the solpugid lashed out at the lizards each time they came close.

Whiptails were also seen to climb into bushes and to dig around stones and plants. While retreating from an observer, one lizard was seen to seek refuge in an ant bed. It quickly emerged with ants clinging to various parts of its body. When picked up, all of the whiptails were heard to emit an audible squeak as recorded for *C. tigris* by Milstead (1959).

The whiptail lizards studied on the Alpine quadrat are representatives of two recognized subspecies, *Cnemidophorus sacki gularis* Baird and Girard and *Cnemidophorus sacki exsanguis* Lowe, which are sympatric at a few localities in the eastern Davis Mountains. The two forms are similar morphologically and in certain behavioral characteristics, but they appear to have different ecological preferences. *C. s. gularis* is typically found in level, prairie areas, while *C. s. exsanguis* is typically found in more rugged habitats (Milstead, 1957a). The localities where the two forms occur sympatrically are near the range extremes of both (western for *C. s. gularis* and eastern for *C. s. exsanguis*), and the habitats are subtypical of both. Whether the two forms include the intergrades of two subspecies, represent two distinct subspecies in an overlap zone, or represent two distinct species is a decision which may be determined only by further study. Should the reader be tempted to draw hasty conclusions, he is reminded that sympatry, especially when it is limited to marginal areas of range, is not by itself sufficient cause for naming two forms as distinct species.

MAMMALIA

Nineteen mammals of three species were captured, marked, and released during the study. Seven of these were recovered at least once for a total of 22 recoveries.

Lepus californicus texanus Waterhouse. Texas Jackrabbit. Individuals of this species were frequently seen on the quadrat, but could not be captured in any of the traps used. Two nests were found during the study and each contained two juveniles. Each nest consisted of scooped-out hollows on the east and west sides of a bush. The young rabbits were found in the west hollow in the mornings and in the east hollow in the evenings. The two juveniles in one nest were marked, but were not recovered.

Perognathus hispidus paradoxus Merriam. Hispid Pocket Mouse. Three females and three males were marked, and three of these were recaptured for a total of eleven recoveries. Two males were recaptured once each and one female was recaptured nine times. The ten records of this female were in four live-mouse traps and the total area (Fig. 1) included only 0.12 acre. It is unlikely that this is the true size of her home range.

Dipodomys merriami merriami Mearns. Four-toed Kangaroo Rat. Five females and six males of this species were captured in live-mouse traps. One female and one male were recaptured twice each, another male was recaptured three times, and another four times. The initial capture and first recapture of the latter male were in the same trap, and the three other recoveries were in an adjacent trap.

Other mammals. Five species of mammals not captured were periodically seen on the quadrat during the study: the cottontail (*Sylvilagus auduboni*), the ground squirrel (*Citellus spilosoma*), the raccoon (*Procyon lotor*), the mule deer (*Odocoileus hemionus*), and the pronghorn antelope (*Antilocarpa americana*). The ground squirrel was the only one of these small enough to be caught in the traps, but that was prohibited by the closure of the traps during daylight hours.

REFERENCES

ANDERSON, ALFRED W. 1949. Early summer foods and movements of the mule deer (*Odocoileus hemionus*) in the Sierra Vieja Range of southwestern Texas. *Tex. J. Sci.*, **1**(4):45-50.

BLAIR, W. FRANK 1940. A contribution to the ecology and faunal relationships of the mammals of the Davis Mountains region, southwestern Texas. *Misc. Publ. Univ. Mich. Mus. Zool.*, **45**:1-39.

———1941. A simple and effective live trap for small animals. *J. Wildlife* Manag., **5**:191-193.

———1950. The biotic provinces of Texas. *Tex. J. Sci.*, **2**(1):93-117.

———1958. Effects of x-irradiation on a natural population of the deer-mouse (*Peromyscus maniculatus*). *Ecology*, **39**:113-118.

——— AND T. E. KENNERLY, JR. 1959. Effects of x-irradiation on a natural population of the wood-mouse (*Peromyscus leucopus*). *Tex. J. Sci.*, **9**(2):137-149.

BURT, WILLIAM HENRY 1943. Territoriality and home range concepts as applied to mammals. *J. Mamm.*, **24**(3):346-352.

DICE, LEE R. 1943. *The Biotic Provinces of North America.* Univ. Mich. Press, Ann Arbor; i-viii, 1-78.

DIXON, KEITH L. 1958. Spatial organization in a population of Nelson pocket mouse. *Southwest Naturalist*, **3**(1-4):107-113.

FITCH, HENRY S. 1958. Natural history of the six-lined racerunner (*Cnemidophorus sexlineatus*). *Univ. Kans. Publ. Mus. Nat. Hist.*, **11**(2):11-62.

HOWARD, WALTER E. 1949. Dispersal, amount of inbreeding, and longevity in a local population of prairie deermice on the George Reserve, southern Michigan. *Contrib. Lab. Vert. Biol. Univ. Mich.*, **43**:1-50.

KING, PHILLIP B. 1937. Geology of the Marathon region of Texas. *U.S. Geol. Surv., Prof. Pap.* **187**.

MCCARLEY, W. HOWARD 1958. Ecology, behavior, and population dynamics of *Peromyscus nuttalli* in eastern Texas. *Tex. J. Sci.*, **10**(2):147-171.

MILSTEAD, WILLIAM W. 1957a. Some aspects of competition in natural populations of whiptail lizards (*genus Cnemidophorus*). *Ibid.*, **9**(4):410-447.

———1957b. Observations on the natural history of four species of whiptail lizards, *Cnemidophorus* (Sauria, Teiidae) in Trans-Pecos Texas. *Southwest Nat.*, **2**(2-3):105-121.

———1959. Drift-fence trapping of lizards on the Black Gap Wildlife Management Area of southwestern Texas. *Tex. J. Sci.*, **11**(2):150-157.

———In press. Competitive relations in lizard populations. *In* Vertebrate Speciation, W. F. Blair ed. Univ. Tex. Press.

NICE, MARGARET MORSE 1941. The role of territory in bird life. *Am. Midl. Nat.*, **26**(3):441-487.

STICKEL, WILLIAM H. AND JAMES B. COPE 1943. The home ranges and wanderings of snakes. *Copeia*, (2):127-136.

YORK, CHRISTOPHER L. 1949. Notes on home ranges and population density of two species of heteromyid rodents in southwestern Texas. *Tex. J. Sci.*, **1**(3):42-46.

Melanism in the Poeciliid Fish, Gambusia affinis (Baird and Girard)[1]

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ABSTRACT: Integumentary melanophores in normally-pigmented *Gambusia affinis* are of two types: a scale melanophore found in the epidermis covering the scales and a stellate micromelanophore which is found in the dermis. Melanistic individuals also possess macromelanophores in the dermis. Melanism appears to be confined to males of the species and the degree of melanism varies greatly. Collections totaling 3,002 fish from three localities in southern Florida contained significantly different percentages of melanistic individuals among the recognizable males. Six F_1 males, progeny of matings of melanistic males with normally-pigmented females, were reared to sexual maturity. All had only normal pigmentation.

The live-bearing top-minnow, *Gambusia affinis* (Baird and Girard), is widely known due to its importance in mosquito control. As Innes (1952) has noted, melanistic individuals occasionally occur in collections of *Gambusia*. This condition is apparently confined to males of the species.

Abnormal melanophores can be the precursors of melanomas (Gordan and Lansing, 1943): Grand, *et al.* (1943) demonstrated essential likenesses in piscine and mammalian melanotic cells *in vitro*. In view of this knowledge and the fact that *Gambusia* occurs so commonly, it is surprising that no works on melanistic *Gambusia* are found in the literature.

The present report deals with the types of integumentary melanophores found in normal and melanistic *Gambusia*, and the frequency of melanistic individuals in collections totaling 3,002 fish from three localities in southern Florida. Some preliminary genetic data are also included.

Methods

Whole mounts of normal and melanistic skin were made using the alcohol dehydrating series and clearing in terpineol. Melanophores were measured in the dispersed phase using an ocular micrometer.

Collections were made with a 15 ft. seine of 3/8 in. mesh (inside measurement, stretched). Since it is probable that some of the very small fish could escape, the collections do not represent a random sample of all sizes. *Gambusia affinis* is 7 to 8 mm, standard length, at birth and the smallest, commonly-occurring size in these collections is 13 mm, although a few fish of 9 to 12 mm were also col-

[1] The writer is grateful to Professors L. C. Gilman, E. R. Rich and L. R. Rivas of the Department of Zoology, University of Miami, Coral Gables, Florida, who offered him aid and helpful criticism during this study.

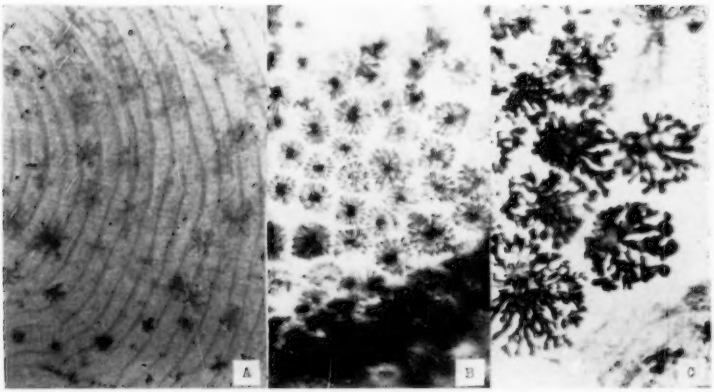

Fig. 1.—Melanophores in *Gambusia affinis*. A. Scale melanophores. B. Dermal micromelanophores. C. Dermal macromelanophores. Magnification 50×.

lected. Individuals were considered males when any anal fin development beyond that of a normal female was noted.

A gravid, normally-pigmented female was collected and placed in a breeding trap in the laboratory. A stock of virgin females was isolated from her progeny and these were mated to melanistic males. The progeny of these matings were raised to maturity in individual gallon jars.

RESULTS AND DISCUSSION

In normally-pigmented *Gambusia*, two types of melanophores are present in the integument: a scale melanophore (Fig. 1A) which is found in the epidermis covering the scales, and a micromelanophore (Fig. 1B) which is found in the dermis. The scale melanophore has fan-like projections which are morphologically distinct from the stellate projections of the micromelanophores. The scale

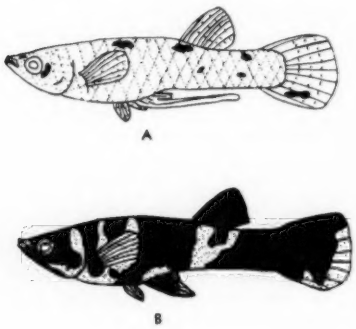

Fig. 2.—Two specimens of melanistic *Gambusia affinis*. A. Mature male, 24 mm standard length. B. Immature male, 18 mm standard length.

TABLE I.—Mean diameters ± standard error of melanophores in *Gambusia affinis*

Melanophore type	No. measured	M ± SE
Scale melanophore	35	.056 ± 0.11 mm
Dermal micromelanophore	50	.074 ± .011 mm
Dermal macromelanophore	19	.146 ± 0.20 mm

melanophore of *Gambusia* appears to be similar to the scale melanophore described by Gilson (1926) for *Fundulus*, by Goodrich (1927) for *Oryzias*, and by Gordon (1931) for *Platypoecilus*.

The micromelanophore of *Gambusia* is a small cell having many thin, delicate projections; there are also more projections per cell in this than in the other types of melanophores. The general morphology of this cell is almost identical with that of the micromelanophores of *Platypoecilus* as described by Gordon (1931). However, the *Platypoecilus* micromelanophore averaged 1.2 mm in diameter while the micromelanophore of *Gambusia* is .07 mm mean diameter.

In addition to the normal types of melanophores discussed above, melanistic *Gambusia* possess macromelanophores (Fig. 1C) in the dermis. These cells are nearly twice the size of the micromelanophores (Table I) and their morphology is quite distinct. Their projections are much thicker and varicose, and are more dichotomous than those of the micromelanophores.

The number of macromelanophores present in melanistic *Gambusia* appears to vary greatly among individuals. Specimens with only six macromelanophores have been collected, while almost totally-black males have also been taken. The degree of melanism does not appear to vary directly with the degree of sexual maturity, as can be seen by the individuals pictured in Figure 2.

Data on the collections of *Gambusia* from southern Florida are

TABLE II.—Collections of *Gambusia affinis*

Collection	Location	Date	Females and Immature males	Normal males	Melanistic males	Totals
1	Irrigation ditch near mouth of Black Creek, Dade Co., Fla.	April 1, 1958	889	121	2	1012
2	Tamiami Canal, Dade Co., Fla.	June 4, 1958	842	156	12	1010
3	Irrigation ditch near Cutler Rd., Dade Co., Fla.	June 17, 1958	646	330	4	980

TABLE III.—Chi-square test of percentage of melanistic males among total males in each collection

Collection	No. males (n)	No. melanistic males (x)	% melanistic males (p)	(p) (x)
1	123	2	1.6260	3.2520
2	168	12	7.1428	85.7136
3	324	4	1.1976	4.7904
	625	18	9.9664	93.7560

$\bar{p} = 2.88$ $\bar{q} = 97.12$ $\overline{pq} = 279.7056$ $\overline{p\Sigma x} = 51.84$ d.f. $= 2$

$x^2 = 14.9857$ $P < .01$

shown in Table II. Collections 1 and 3 came from narrow irrigation ditches with stagnant, turbid water. Collection 2 came from a wide clear stream having apparently good water flow.

The data were tested for significant differences in the percentage of melanistic males among the recognizable males from each locality (Table III).

Chi-square was computed using the Brandt and Snedecor modification (Snedecor 1948) of:

$$X^2 = \frac{100(\Sigma px - \frac{v}{p}\Sigma x)}{\overline{pq}}$$

where: p = percentage of melanistic individuals among recognizable males collected,

x = number of melanistic individuals among recognizable males collected,

n = number of males in each sample,

$\bar{p} = \Sigma x/\Sigma n$

$\bar{q} = 1-\bar{p}$

These percentages differed significantly and Collection 2 is seen to have contributed the aberrant values. Barney and Anson (1921) and Geiser (1924) have shown that sex ratio varies with time and place in *Gambusia;* it is thus not feasible to compare the percentage of melanism among all the fish collected from place to place. Comparing percentage melanism among the recognizable males is also not completely satisfactory since an unknown quantity of immature males is included in the fish classed as females. The error thus introduced

cannot be great, however, since mature and maturing males of 13 to 15 mm, standard length, occurred in all three collections, and a very small proportion of the fish classed as females were below this size range.

A total of 16 F_1 progeny from two matings of melanistic males with normal females were brought to sexual maturity. Six of these were males, all of which were normally-pigmented. These results might appear to negate a hypothesis of holandric inheritance of melanism. However, the expression of the melanistic phenotype may possibly be modified by certain ecological factors, particularly temperature, and since the F_1 males were not reared under controlled physical conditions, these results do not conclusively exclude holandric inheritance. In the same way, differing ecological conditions which may affect expression of the melanistic phenotype, rather than differing gene frequencies, may account for the variation found in the frequency of melanistic individuals in the collections reported here.

In addition to the hypothesis of holandric inheritance, there are, of course, other genetic hypotheses to be investigated.

REFERENCES

BARNEY, R. L. AND B. J. ANSON 1921. Seasonal abundance of the mosquito-destroying top-minnow *Gambusia affinis*, especially in relation to male frequency. *Ecology*, **2**:53-69.

GEISER, S. W. 1924. Sex ratios and spermatogenesis in the top-minnow, *Gambusia holbrooki* Grd. *Biol. Bull.*, **47**:175-212.

GILSON, A. S., JR. 1926. Melanophores in developing and adult *Fundulus*. *J. Exptl. Zool.*, **45**:415-419.

GOODRICH, H. B. 1927. A study of the development of Mendelian characters in *Oryzias latipes*. *Ibid.*, **49**:261-267.

GORDON, M. 1931. Morphology of the heritable color patterns in the Mexican killifish, *Platypoecilus*. *Am. J. Cancer*, **15**:732-787.

——— AND W. LANSING 1943. Cutaneous melanophore eruptions in young fishes during stages preceding melanotic tumor formation. *J. Morphol.*, **73**:231-245.

GRAND, C. G., M. GORDON, AND G. CAMERON 1943. Neoplasm studies VIII: Cell types in tissue of fish melanotic tumors compared with mammalian melanomas. *Cancer Res.*, **1**:660-666.

INNES, W. T. 1952. *Exotic Aquarium Fishes*. 14th ed. Innes Publishing Co., Philadelphia. 521 pp.

SNEDECOR, G. W. 1948. *Statistical Methods*. 4th ed. Iowa State College Press, Ames. 485 pp.

The Marsh Flies of Idaho and Adjoining Areas (Diptera: Sciomyzidae)[1]

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ABSTRACT: Keys and distributional data are given for the 16 genera and 75 species of marsh flies known to occur in the northwestern states and provinces of Montana, Utah, Idaho, Washington, Oregon, Alberta and British Columbia. Detailed collection records are given only for Idaho, but the place of collection is given for the other states and provinces. A general discussion of Idaho as a habitat for marsh flies is presented, and important collecting stations within the state are described.

Introduction

Although recent papers by Steyskal (1950, 1954a, 1954b, 1954c, 1954d, 1956, 1957, 1959), Berg (1953), Foote (1959) and Foote *et al.* (1960) present information on one or more species of Sciomyzidae occurring in northwestern North America, there has been no comprehensive publication dealing with the family in the Pacific Northwest since the revisions by Melander (1920) and Cresson (1920). In the present paper are presented keys to the 16 genera and 70 species and subspecies of marsh flies occurring in the northwestern states and provinces of Montana, Utah, Idaho, Washington, Oregon, Alberta and British Columbia. Although detailed distribution records are given only for Idaho, some information on the local occurrence of the flies in other states and provinces is also included.

Papers by Berg (1953), Berg *et al.* (1959), Foote (1959) and Foote *et al.* (1960) present evidence that many, if not all, sciomyzid larvae kill and feed upon aquatic and terrestrial snails. A continuum of feeding habits has been found, with some species having larvae that are free-living aquatic predators, while others have terrestrial parasitoid larvae. Larvae of many species have feeding habits that are intermediate between these two extremes. The author is presently engaged in a study of the biology of the species occurring in the Pacific Northwest and has accumulated additional information on the snail-killing activities of the larvae. However, little of this biological information is included in the present paper because data for some species are still fragmentary and the biology of many species has not yet been investigated.

Acknowledgments.—Although most of the distributional data for Idaho were obtained by the author, several other individuals made important contributions. The members of the Department of Entomology, University of Idaho, have been very co-operative with the sciomyzid survey of the state. H. C. Manis,

[1] Published with the approval of the Director of the Idaho Agricultural Experimental Station as Research Paper No. 484.

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head of the department, by his continuing interest in the study stimulated the publication of this report. W. F. Barr collected specimens in many regions of the state and provided information as to productive collecting sites. A. R. Gittins, survey entomologist, and R. W. Portman, extension entomologist, provided transportation to many localities throughout the state and contributed specimens collected during their travels. Appreciation is also due to several curators of collections in states and provinces surrounding Idaho. George F. Ball (University of Alberta), Frank Hasbrouck (Oregon State University), George F. Knowlton (Utah State University), Maurice T. James (Washington State University) and G. G. E. Scudder (University of British Columbia) freely loaned the specimens under their care. Finally, appreciation is extended to George C. Steyskal, the leading American authority on the Sciomyzidae, for his co-operation in the determination of certain difficult species, especially within the genus *Pherbellia*.

GENERAL ACCOUNT

Located on the western flanks of the Northern Rocky Mountains, the state of Idaho shows a diversity of physiography, climate, life zones, and biotic provinces. Fenneman (1931) recognizes four physiographic provinces within the state. The mountainous sections of northern and central Idaho are in the Northern Rocky Mountain Province. This province is delimited on the south by the lava plains along the Snake River and in the west by the Columbia Plateau. Northward and eastward the province extends beyond the boundaries of the state. The elevation within this large area ranges from less than 3000 feet on the west where the Salmon River leaves the province to over 12,000 feet at Mt. Borah near the southern border. The rocks making up the mountains are almost uniformly resistant, and much of the mountainous terrain is characterized by an accordance of crest levels that appears to have resulted from the dissection of an old plateau surface. Long, linear ranges are relatively uncommon. The valleys are usually steep walled and in some areas form extensive basins (e.g. Stanley Basin north of Sun Valley and the basin surrounding Idaho City.) Near the southern border of the province where the mountains abut against the Snake River lava plains, long, linear valleys separated by ranges of lofty mountains are found. On the border between Idaho and Montana the Bitterroot Range rises to elevations exceeding 9000 feet with an occasional peak rising to 10,500 feet. In the north near the Canadian border the mountains rarely exceed 7000 feet and are separated into more or less north-south ranges by sizeable river valleys.

Lying along the Idaho-Wyoming border is a mountainous area that Fenneman includes in the Middle Rocky Mountain Province. In Idaho this province includes a series of nearly parallel, north-south ranges (e.g. Bear River Range, Caribou Range, Snake River Mountains) that are bounded on the west by the Snake River Plain and the Basin and Range Province. The crests reach elevations between 9000 and 10,000 feet. Located east of the Bear River Range is an extensive marshy plain bordering Bear River and Bear Lake.

The Columbia Plateau Province enters the state from the west and

in southern Idaho includes the extensive area of lava plains located along the Snake River. The rocks underlying this province are mainly lava flows ranging from 10 to 100 feet in thickness. Near the western boundary of the state along the Snake River approximately 4000 feet of lava beds are exposed. In western Idaho lake sediments are interbedded with the lava flows. The topography is generally flat to slightly undulating, although cliffs are abundant along the larger streams and numerous buttes and lava cones project above the general plateau surface. The elevation on the lava plains ranges from less than 2500 feet in the west to nearly 6000 feet in the northeast. Traversing the extensive lava plains is the great canyon of the Snake River. South of this river and near the Oregon border are found the Owyhee Mountains, a north-south range that is about 30 miles long and surrounded by lava plains. The mountains reach elevations exceeding 8000 feet with the plateau surface sloping away in all directions from the high center. Along the western border of Idaho near the southeastern corner of Washington is an area of gently rolling hills called the "Palouse Country." The soil in this region is a very fine textured, deep loess deposit blown in from arid lands to the west.

The southcentral portion of the state extending east to the foot of the Bear River Range is included in the Basin and Range Province. Within this area the topography consists of isolated, parallel ranges separated by broad, arid, nearly level basins. The rocks underlying the basins are mostly sedimentary, while the higher mountains frequently have a core of igneous rocks. At the foot of the mountains are extensive alluvial fans and slopes which gradually merge with the flat plains.

Carter (1941) presents a general account of the climatic conditions existing within the state. He notes that altitude, not latitude, is of primary importance in influencing temperature and precipitation. Lying in a region of prevailing westerly winds, the state is greatly affected by the ameliorating influence of the Pacific Ocean and has a climate milder than its geographic position and altitude would otherwise indicate. The Continental Divide serves as a partial barrier to the cold fronts moving down from the Canadian Northwest. In general, there is a gradual rise in the annual precipitation from the relatively low-lying Columbia Plateau Province to the high mountains of central and eastern Idaho. The average annual precipitation ranges from 10 inches or less along the Snake River to more than 40 inches in the extreme northeastern counties. Much of the state lying in the Panhandle near the Washington-Idaho border receives 20 to 30 inches annually while the southern and eastern counties receive 10 to 20 inches per year. Over practically the entire state January is the wettest month and July and August are the driest. From August on, there is a gradual, but steady rise in the monthly precipitation. Thirty-three percent of the precipitation occurs during the winter months; 27 percent in March-May; 15 percent in June-August and 25 percent during the fall.

The last killing frost usually occurs during May in much of the Panhandle, along the Snake River and in the southern counties. Locally in the Panhandle, at low elevations along the Idaho-Wyoming border and in parts of the interior, the average date occurs in June. At high elevations in mountainous terrain, heavy frosts may occur in every month of the year. The first killing frost in fall comes during August at high elevations along the Idaho-Wyoming border and in parts of the interior, but in the Boise Valley and in much of the Panhandle, it is delayed until October. In the remainder of the state, it usually occurs sometime in September.

According to Dice (1943) four biotic provinces are found in Idaho. The extensive sage-brush covered plains of southern Idaho belong to the Artemisian province. Coinciding with the Northern Rocky Mountain physiographic province is the Montanian province, while the Coloradan province is co-extensive in Idaho with Fenneman's Middle Rocky Mountain Province. The "Palouse Country" is included in the Palousan province. Knowledge of the distribution of sciomyzids in Idaho is still too incomplete to determine whether any of these biotic provinces have characteristic faunas.

Mason (1957) presents a classification of aquatic habitats based on his studies of the marshlands of California. Following his classification, specimens of sciomyzids were taken in Idaho from margins of permanent fresh water lakes, ponds and marshes, vernal pools and marshes and from streamside marshes. Those sciomyzid species whose larvae are aquatic predators (e.g. *Sepedon fuscipennis*) are found predominantly in the more permanent marshy situations such as those found around lakes and ponds. Those species whose larvae attack stranded aquatic snails (e.g., *Atrichomelina pubera*) occur most commonly in habitats where the water level is unstable. The larvae of *Sciomyza* spp. develop in species of *Oxyloma,* the so-called amphibious snails that are found commonly on emergent vegetation in marshy habitats. No sciomyzid known to have its larval stages associated with strictly terrestrial snails has been found in Idaho.

COLLECTING STATIONS

Several collecting stations were established in various habitats throughout the state. As these stations will be utilized in future studies, they are described in some detail below.

Copeland, Boundary County.—This station consists of two small ponds located in borrow pits along both sides of the Great Northern Railway just north of the town. The pond situated on the west side of the tracks is mostly unshaded and has considerable development of emergent vegetation. Its shores are covered with species of rushes, sedges, grasses, shrubs (especially red-osier dogwood, *Cornus sericea* L.) and a few small trees (mostly willows, *Salix* spp. and trembling aspen, *Populus tremuloides* Michx.). Aquatic snails common in the pond are *Lymnaea palustris* (Muller) and *Helisoma* sp. Among the

sciomyzids swept from the herbaceous vegetation bordering the ponds were *Sciomyza simplex, Pherbellia griseola* and *Hedroneura rufa.*

The somewhat larger pond east of the tracks contains relatively little emergent vegetation, but is bordered by a dense zone of herbaceous plants composed largely of sedges, jewelweed (*Impatiens aurella* Rydb.), various species of shade-loving asters, nettles (*Urtica* spp.), cocklebur (*Xanthium strumarium* L.), beggar-ticks (*Bidens cernua* L.), rattlesnake-root (*Prenanthes sagittata* Gray) and Joe-pye-weed (*Eupatorium maculatum* L.). Shrubs are abundant, especially the red-osier dogwood, and the margins of the pond are well-shaded by such deciduous trees as willow, cottonwood (*Populus trichocarpa* T. & G.) and box-elder maple (*Acer negundo* L.). In addition to *Lymnaea* and *Helisoma* snails, species of *Gyraulus* and *Physa* are found. Among the more interesting sciomyzids collected around the margins of the pond were *Pherbellia griseola, P. vitalis, Antichaeta melanosoma* and *Sepedon spinipes americana.*

Eight miles north of Sandpoint, Bonner County.—This is a small, partially wooded swamp situated in a borrow pit between U. S. Highway 95 and the Great Northern Railway. The area is partially shaded by small alders, willows, and box elder maples with an understory composed mostly of young trees and red-osier dogwood. The herbaceous vegetation is lush and forms a dense cover over the permanently saturated soil. Common herbs are bracken fern (*Pteridium aquilinum* var. *languinosum* (Bong.) Fernald), rushes (*Juncus* spp.), sedges (mostly *Carex* sp.), jewelweed, beggar-ticks and cocklebur. In addition to a shallow pond of 8 to 20 feet diameter, there are several small depressions that contain a few inches of water during the spring and early summer. Snails present in the area included *Lymnaea palustris,* L. *humilis* Say, *Physa gyrina* Say, *Gyraulus* sp. and *Oxyloma* sp. Among the more interesting sciomyzids collected by sweeping the hydrophilic vegetation were *Pherbellia schoenherri, Renocera cyathiformis, Tetanocera plebeia* and *T. unicolor.*

Three miles south of Worley, Kootenai County.—The collecting station is located in a small marshy area lying on the west side of U. S. Highway 95 near a small stream. Standing water up to a foot in depth covers much of the area during spring and early summer, but the marsh becomes completely dry by late July. Along the western margin of the marsh is a mixed stand of second-growth deciduous and coniferous trees. Trembling aspen, willows, and ponderosa pine (*Pinus ponderosa* Dougl.) are especially numerous and offer some shade. Growing in portions of the marsh itself is a dense shrub cover composed mostly of white spiraea (*Spiraea betulifolia* Pall.). Hydrophilic herbaceous vegetation is abundant and is composed of such forms as grasses, rushes, sedges, rice-root (*Fritillaria lanceolata* Pursh), hellebore (*Veratrum viride* Alt.), blue-eyed grass (*Sisyrinchium inflatum* Suksd.) buttercups (*Ranunculus* spp.), marsh cinquefoil (*Potentilla arguta* Pursh), monkey-flower (*Mimulus* sp.), *Downingia elegans* (Dougl.), beggar-ticks, tickseed (*Coreopsis atkinsoniana* Dougl.) and

squaw-weed (*Senecio* sp.). Snails are abundant and usually are stranded on the wet mud as the water recedes during the summer months. Common species present are *Lymnaea palustris, L. humilis* and *Physa* sp. Among the more interesting sciomyzids collected were *Pherbellia vitalis, Sepedon neili* and *Tetanocera plebeia.*

Robinson's Lake, Latah County.—This is a small, artificial lake located approximately eight miles east of Moscow. The lake was formed during the 1930's by the construction of a dam across a small stream. Although the eastern and western shores are wooded (mostly ponderosa pine), the greater share of the lake is unshaded. The greatest depth is found near the dam at the south end while the north end bordering the inlet stream is shallow and supports a lush growth of emergent vegetation. Here, cat-tails (*Typha latifolia* L.), sedges (mostly *Carex* spp.) and rushes form fairly dense stands. Immersed species abundant in the shallower water near the shoreline include Canada waterweed (*Anacharis canadensis* (Michx.) Planch), hornwort (*Ceratophyllum demersum* L.), water milfoil (*Myriophyllum verticillatum* L.), and pondweed (*Potamogeton* spp.). Duckweed (*Lemna minor* L.) frequently covers the water's surface where the depth does not exceed two feet. Lying along the inlet stream is an extensive mud flat covered by a lush growth of reed canary grass (*Phalaris arundinacea* L.). Aquatic snails are very abundant and include such species as *Lymnaea palustris, L. humilis, Physa gyrina, Helisoma* sp. and *Gyraulus* sp. Among the more interesting species of sciomyzids collected were *Pherbellia grisescens, Tetanocera plebeia, T. robusta* and *T. soror.*

Dixie, Elmore County.—This station is a relatively open expanse of marshland located approximately one mile southwest of the town. The area is largely unshaded and lies in a shallow depression surrounded by low, sagebrush-covered hills. A small stream meanders through the marsh, but most of the surface water seems to result from seepage along the margins of the hills. Although the soil remains saturated throughout the year, standing water is present only during the spring and early summer. Herbaceous, hydrophilic vegetation is abundant, but is composed mostly of numerous species of sedges and rushes. Other herbs present include blue-eyed grass, duckweed, buttercups, asters, balsam root (*Balsamorhiza* sp.) water-cress (*Rorippa nasturtium - aquaticum* (L.) S. & T.) and marsh cinquefoil. Snails are abundant and include such secies as *Lymnaea humilis, Physa* sp., *Gyraulus* sp. and *Oxyloma* sp. Interesting sciomyzids collected were *Hedroneura connexa, Sepedon borealis,* and *Tetanocera latifibula.*

Stanley Basin, Blaine and Custer Counties.—This is a high mountain valley lying along the headwaters of the Salmon River. The valley is bounded on the west by the Sawtooth Mountains, on the southeast by the Boulder Mountains and on the north by the Salmon River Mountains. The collecting station was established along the east shore of the river near U.S. Highway 93, approximately ten miles

north of Galena Summit. The area sampled includes several small ponds evidently formed by overflow from the main stream. Small alders and willows give some shade, but most of the habitat is unshaded. Aquatic emergent vegetation is abundant and is composed mostly of various species of sedges and rushes along with some cattail and water cress. The margins of the ponds support lush stands of sedges, rushes, and grasses along with a variety of other hydrophilic herbs. Shrubs are fairly common with red-osier dogwood and white spiraea being especially numerous. Common snails are *Lymnaea palustris, L. humilis, Physa* sp. and *Oxyloma sp.* Among the numerous sciomyzids collected by sweeping the herbaceous vegetation were *Sciomyza dryomyzina* (only Idaho record), *Hedroneura connexa, Renocera cyathiformis, R. johnsoni* and *Tetanocera latifibula.*

Ten miles west of Mack's Inn, Fremont County.—This station is located approximately 100 yards north of a gravel road running between Kilgore and U.S. Highway 20. It consists of a small marsh of less than one-half acre lying in a slight depression on the nearly level plains west of Mack's Inn. Although the water level decreases steadily as summer advances, the soil of the marshy area remains moist throughout the summer. The vegetation consists almost entirely of a fairly dense stand of rushes and sedges. Snails are abundant and are frequently stranded as the water level recedes during the late summer. Species found in the marsh include *Lymnaea palustris, L. humilis, Helisoma* sp. and *Physa* sp. Among the more interesting sciomyzids collected by sweeping the marsh vegetation were *Atrichomelina pubera, Pherbellia grisescens* and P. *vitalis.* Over 500 specimens of *P. vitalis* were collected during an hour of intensive collecting on July 17, 1959.

Swan Lake, Targhee National Forest, Fremont County.—This station consists of a small, senescent lake located on the west side of U.S. Highway 20 approximately 15 miles south of Mack's Inn. The lake does not exceed 10 feet in depth and the greater portion of its expanse is less than two feet in depth. Immersed, floating and emergent vegetation is abundant, and very little open water is present. Immersed plants include Canada waterweed, water milfoil, hornwort, naiad (*Najas flexilis* Willd.) and pondweed. Floating species present, among others, are yellow pond-lily (*Nuphar polysepalum* Engelm), watershield (*Brasenia Schreberi* Gmel.) and duckweed. Emergent plants form dense stands in the shallower water and include such species as hydrophilic sedges and rushes, arrowhead (*Sagittaria latifolia* Willd.) water plantain (*Alisma Plantago-aquatica* L.) cat-tail and bur-reed (*Sparganium* sp.). The lake is nearly encircled by a forest composed almost entirely of coniferous species. The shallower areas of the lake support a rich population of aquatic snails including *Lymnaea palustris, Helisoma* sp., *Physa gyrina* and *Gyraulus* sp. among others. Individuals of the so-called amphibious snail *Oxyloma* sp. are abundant on the leaves and stems of the emergent plants. Some of the more interesting species of sciomyzids collected were

Sciomyza simplex, Pherbellia nana, Pteromicra nigrimana, Tetanocera latifibula and *T. mesopora.*

Bear Lake, Bear Lake County.—The collecting station was located in an extensive marshy area approximately four miles west of the town of Mud Lake and one-half mile north of the gravel road leading east from U.S. highway 89 to the town. The flood plain bordering the Bear River north of the lake is low-lying, poorly drained and includes many extensive marshes. The collecting station was placed at the edge of one of these marshy areas. The marsh is completely unshaded and supports a rich stand of hydrophilic vegetation composed primarily of numerous species of sedges (mostly *Carex* spp.) and rushes. At the time of collection in mid-July the water depth was less than one foot, and extensive areas lacked standing water, although the soil was water-logged. Aquatic snails are abundant and include such common genera as *Lymnaea, Physa, Helisoma* and *Gyraulus.* Many snails are stranded on the wet soil as the water level recedes during the summer months. A very interesting group of sciomyzid species was taken including some forms not collected elsewhere in the state (e.g., *Pherbellia obtusa* and *Sepedon anchista*).

In addition to the several collecting stations described above, specimens are available from numerous other localities throughout the state. In order to avoid unnecessary repetition in the systematic account these localities are listed by county below.

Bear Lake Co.: Bear Lake, Fish Haven, Montpelier; *Benewah Co.:* Rocky Point on Lake Chatcolet; *Bingham Co.:* Aberdeen; *Blaine Co:* Gannet, Hailey; *Bonner Co.:* Granite Lake, 12 miles N. of Granite, Sandpoint, Westmond; *Boundary Co.:* Bonners Ferry, Copeland, Priest Lake, Priest River Forest Experiment Station; *Butte Co.:* Arco, near Craters of the Moon National Monument.

Camas Co.: Fifteen miles S. of Fairfield, Hill City; *Canyon Co.:* three miles W. of Parma; *Caribou Co.:* Bancroft, Wayan; *Cassia Co.:* Declo, Elba-Basin Pass, Emery Canyon located 12 miles SE. of Oakley; *Clark Co.:* Kilgore, 2 miles E. of Spencer; *Clearwater Co.:* Elk River, Pierce; *Custer Co.:* Challis, 14 miles N. of Mackay, Stanley Basin approximately 10 miles N. of Galena Summit, Stanley.

Elmore Co.: Dixie, Little Camas Reservoir; *Fremont Co.:* Henry's Lake, 10 miles W. of Mack's Inn, Swan Lake in Targhee National Forest; *Gooding Co.:* Hagerman; *Idaho Co.:* 12 miles S. of Pollock; *Jefferson Co.:* Roberts; *Jerome Co.:* Hazelton; *Kootenai Co.:* Hauser Lake, 3 miles S. of Worley.

Latah Co.: Three miles S. of Deary, 4 miles E. of Genesee, Kendrick, Laird Park near Harvard, Lewiston Grade, Moscow, Moscow Mountain, Robinson's Lake, 5 miles N. of Troy, Vassar Meadows near Deary; *Lemhi Co.:* two miles N. of Gilmore, Salmon; *Lewis Co.:* Craigmont; *Lincoln Co.:* Dietrich, 4 miles E. of Shoshone, Star Lake; *Madison Co.:* Sugar City; *Nez Perce Co.:* Spalding.

Owyhee Co.: Bruneau, Hot Creek Falls; *Payette Co.:* Fruitland; *Power Co.:* Massacre Rocks; *Shoshone Co.:* Kellogg; *Twin Falls Co.:* Clover, Rock Creek Ranger Station in Sawtooth National Forest, Rogerson; *Valley Co.:* Donnelly.

SYSTEMATIC ACCOUNT

The family Sciomyzidae is distinguished from other acalyptrate Diptera by the following combination of characters: costa entire, not broken; subcosta complete, free from vein R_1 distally and ending in the costa; first posterior cell open, not narrowed apically; oral vibrissae absent; postvertical bristles diverging; one or more tibiae with preapical bristles; femora with bristles.

Certain structural characteristics require explanation before the keys to genera and species can be used properly. Species of the subfamily Sciomyzinae have a strong bristle on the propleuron immediately above the base of the fore coxa, but in the genus *Atrichomelina* this bristle is very fine and thin. In the Tetanocerinae the propleura have only small clusters of short, fine hairs. The preapical tibia bristles may be single (Fig. 11) or double (Fig. 12) and may at times be confused with the apical bristles. Usually, however, they are distinctly separated from the apical bristles and easily recognizable. The vallar bristles, if present, are situated on a low, narrow ridge on the pteropleuron just below the base of each wing. The supraspiracular convexity is a low swelling located antero-dorsad of the posterior spiracle and posterior to the base of each wing. Other structures mentioned in the keys are illustrated and need no additional comment here.

In certain genera, especially *Pherbellia* and *Dictya,* the definitive species characters are found in the male genitalia. In order to view the important structures, the posterior tip of the abdomen must be removed, placed in hot 10 per cent potassium hydroxide for a minute or so, washed in water and then spread apart. In the present paper an attempt has been made in the keys to use non-genitalic characters as much as possible, but in the genus *Dictya* this has proved impossible and reference to the male genitalia has been necessary. For figures of the male genitalia in other genera of sciomyzids the reader should refer to the numerous papers by Steyskal.

The genus *Limnia* is in great need of revision, but until that has been done it seems best merely to modify Melander's (1920) key even though some of his species are obviously composite forms. The genus *Pherbellia* is currently being revised by Steyskal, and six new species discovered in Idaho will be described by him in a future publication.

KEY TO GENERA

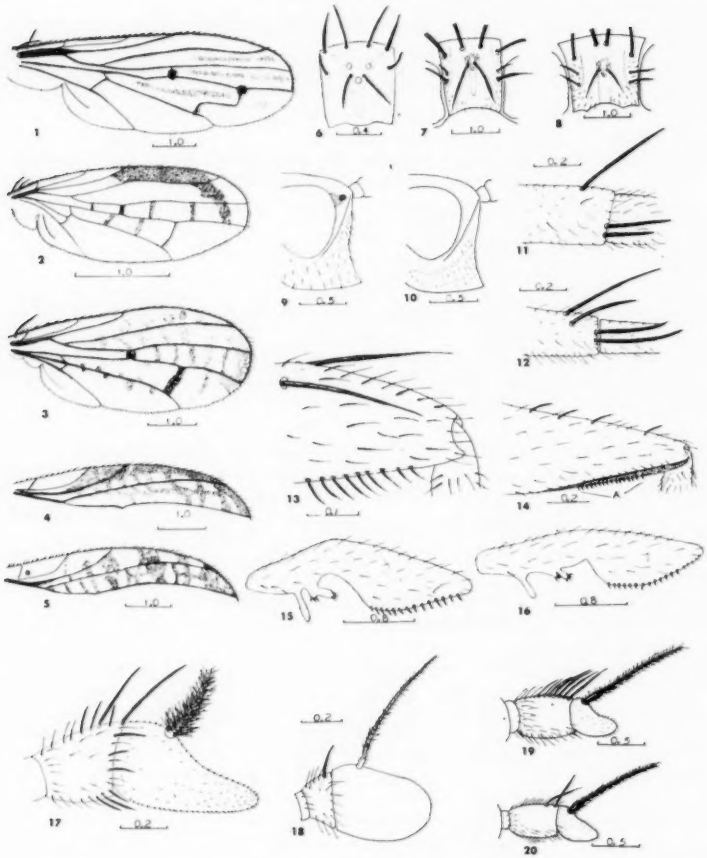
1. Propleuron with strong bristle present above base of fore coxa, if bristle is inconspicuous then first segment of fore tarsi is whitish and contrasts strongly with remaining segments (Sciomyzinae) 2
   Propleuron without strong bristle; first segment of fore tarsi not strongly contrasting with remaining segments (Tetanocerinae) 6
2. Fore tibiae with two preapical bristles ..... *Sciomyza* Fallén
   Fore tibiae with one preapical bristle 3
3. Anal vein not reaching wing margin; body length under 2.5 mm ..... *Colobaea* Zetterstedt (one sp. - *americana* Steyskal)

Anal vein clearly reaching wing margin; body length usually over 2.5 mm 4

4. Propleural bristle inconspicuous; first segment of fore tarsi whitish, fore coxae without bristles .....*Atrichomelina* Cresson (one sp. - *pubera* Loew)
Propleural bristle well-developed; fore coxae with one or more strong bristles 5
5. Body mostly shining black; frons usually entirely shining .....*Pteromicra* Lioy
Body never shining black, usually grayish to yellowish in color; frons not wholly shining .....*Pherbellia* Desvoidy
6. Vallar bristles present 7
Vallar bristles absent 8
7. Arista with blackish hair; midfrontal stripe very narrow .....*Trypetoptera* Hendel (one sp. - *canadensis* Macquart)
Arista with whitish hair or pubescence; midfrontal stripe broader, about one-third width of frons .....*Limnia* Desvoidy
8. Ocellar bristles absent, postocellar bristles well-developed 9
Both ocellar and postocellar bristles well-developed 10
9. Frons with two fronto-orbital bristles; posterior cross vein bisinuate .....*Hedria* Steyskal (one sp. - *mixta* Steyskal)
Frons with only one fronto-orbital bristle; posterior cross vein arcuate .....*Sepedon* Latreille
10. Hind tibiae with two strong preapical bristles (Fig. 12) .....*Antichaeta* Haliday
Hind tibiae with only one strong preapical bristle (Fig. 11) 11
11. Second antennal segment less than one-third length of third segment (Fig. 18) .....*Renocera* Hendel
Second antennal segment at least one-half length of third segment 12
12. Arista with long blackish hairs 13
Arista with whitish hairs or pubescence 15
13. Wings mostly hyaline, usually without dark reticulations; body uniformly yellowish to reddish-brown; mesopleura bare; face without central black spot .....*Tetanocera* Dumeril
Wings heavily marked with blackish spots and reticulations; body brown with numerous blackish spots and elongate markings; mesopleura with bristles 14
14. One fronto-orbital bristle; face with central black spot .....*Dictya* Meigan
Two fronto-orbital bristles; face without central black spot .....*Hoplodictya* Cresson (one sp. - *spinicornis* Loew)
15. Presutural dorsocentral bristle absent; posterior cross vein strongly bisinuate; wings with dark shadings, but never reticulate with black (Fig. 1) .....*Hedroneura* Hendel
Presutural dorsocentral bristle present; posterior crossvein arcuate; wings densely reticulate with black .....*Dictyacium* Steyskal (one sp. - *firmum* Steyskal)

Genus *Pherbellia* Desvoidy

1. Mid-frontal stripe long, reaching at least two-thirds distance to anterior margin of frons (Fig. 6) 2
Mid-frontal stripe shorter, reaching approximately one-half distance to anterior margin of frons 4
2. Wings heavily spotted with black .....*schoenherri* (Fallén)
Wings mostly hyaline 3
3. Mesopleura bare; two parafrontal bristles .....*tenuipes* (Loew)



Figs. 1-20.—Anatomical structures important to identification (all measurements in mm). 1.—Wing of *Hedroneura connexa* Steyskal. 2.—Wing of *Pherbellia nana* (Fallén). 3.—Wing of *Tetanocera valida* Loew. 4.—Costal area of wing of *Limnia pubescens* (Day). 5.—Costal area of wing of *Limnia boscii sparsa* (Loew). 6.—Frontal region of *Pherbellia grisescens* (Meigen). 7.—Frontal region of *Tetanocera ferruginea* Fallén. 8.—Frontal region of *Tetanocera plebeia* Loew. 9.—Lateral view of head of *Tetanocera nanciae* Brimley. 10.—Lateral view of head of *Tetanocera mesopora* Steyskal. 11.—Hind tibia of *Renocera cyathiformis* Melander. 12.—Hind tibia of *Antichaeta testacea* Melander. 13.—Hind femur of *Tetanocera montana* Day. 14.—Fore femur of *Pteromicra nigrimana* Meigen: a, pecten. 15.—Hind femur of *Sepedon anchista* Steyskal. 16.—Hind femur of *Sepedon armipes* Loew. 17.—Antenna of *Tetanocera soror* Melander. 18.—Antenna of *Renocera cyathiformis* Melander. 19.—Antenna of *Limnia pubescens* (Day). 20.—Antenna of *Limnia boscii sparsa* (Loew).

Mesopleura with setae over most of surface; one parafrontal bristle .... *grisescens* (Meigen)
4. Mesopleura with row of short bristly hairs along posterior margin 5
Mesopleura bare 6
5. Wings with costal border yellow, costa, first and second veins yellowish, remaining veins brown; pteropleura with short bristly hairs only .... *albocostata* (Fallén)
Wings without yellowish costal border, all veins brown; pteropleura with two conspicuous bristles in addition to shorter bristly hairs .... *griseola* (Fallén)
6. Marginal cell of wing extensively darkened, submarginal cell with dark cloud near apex, first posterior cell with approximately three transverse dark bars (Fig. 2) ..... *nana* (Fallén)
Wing membrane mostly hyaline, never with numerous transverse bars in first posterior cell 7
7. Anterior legs extensively black; thorax mostly grayish ..... *vitalis* (Cresson)
Anterior legs reddish-brown, thorax reddish-brown ..... *obtusa* (Fallén)

Genus *Pteromicra* Lioy

1. Fore femora without pecten (series of closely spaced spinules located apically on antero-ventral side of femora); pteropleura with at least two longer bristles in addition to shorter bristly hairs; basal segment of fore tarsi whitish ..... *perissa* Steyskal
Fore femora with pecten (Fig. 14); pteropleura with cluster of short, bristly hairs only; basal segment of fore tarsi blackish 2
2. Palpi wholly yellow; one fronto-orbital bristle 3
Palpi blackish, at least apically 5
3. Thorax wholly black, head mostly black ..... *nigrimana* (Meigen)
Thoracic pleura mostly yellowish, head frequently extensively yellow 4
4. Wing cross veins not darkened; last segment of fore tarsi of female whitish ..... *apicata* (Loew)
Cross veins bordered with grayish; last one or two (male) or three (female) segments of fore tarsi whitish ..... *pectorosa* (Hendel)
5. Arista whitish, third antennal segment black; apical two or three segments of fore tarsi whitish ..... *leucothrix* Melander
Arista blackish, third antennal segment reddish; fore tarsi wholly black ..... *melanothrix* Melander

Genus *Sciomyza* Fallén

1. Mesopleura with at least two strong bristles posteriorly in addition to numerous shorter bristly hairs; ventral half of pleura pruinose; dorsum of mesonotum grayish with four darker stripes; fore femora usually wholly yellow ..... *simplex* Fallén
Mesopleura with only few fine, short hairs posteriorly; ventral half of pleura not pruinose, mesonotal dorsum shining reddish-brown; fore femora usually blackened on apical half or more ..... *dryomyzina* Zetterstedt

Genus *Antichaeta* Haliday

1. Body mostly shining black ..... *melanosoma* Melander
Body reddish yellow, never shining black 2
2. Third antennal segment yellow basally, blackish apically ..... *sp. A.*
Third antennal segment wholly yellow 3
3. Thoracic dorsum grayish to blackish ..... *robiginosa* Melander
Thoracic dorsum yellowish ..... *testacea* Melander

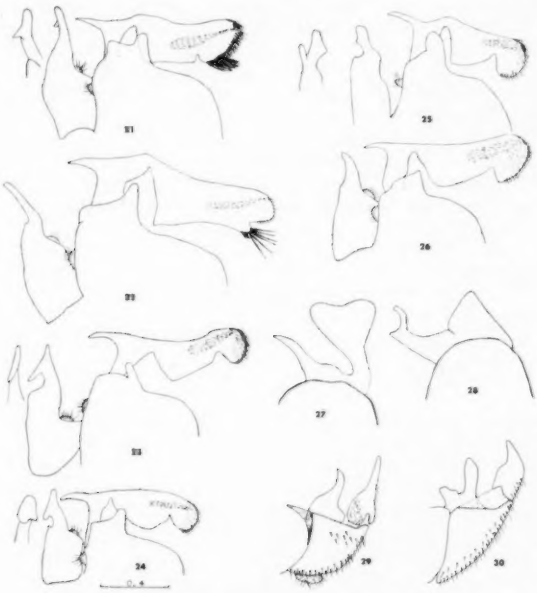
Genus *Dictya* Meigen

MALES

1. Surstylus with apical brush of long bristles (Fig. 21) 2
   Surstylus with short bristles only 3
2. Pregonite with preterminal lobe (Fig. 21) .....*pictipes* (Loew)
   Pregonite without preterminal lobe (Fig. 22) .....*borealis* Curran
3. Pregonite with expanded preterminal lobe (Fig. 24) 4
   Pregonite gradually tapering, without preterminal lobe (Fig. 26) 6
4. Pregonite short, strongly bent, preterminal lobe reduced to small point (Fig. 25) .....*incisa* Curran
   Pregonite longer, not strongly bent, preterminal lobe well-developed 5
5. Preterminal lobe long and narrow in anterior view (Fig. 23) .....*stricta* Steyskal
   Preterminal lobe broadly expanded (Fig. 24) .....*expansa* Steyskal
6. Prosternum with hairs .....*umbroides* Curran
   Prosternum bare .....*montana* Steyskal

Genus *Hedroneura* Hendel

1. Wing with brownish cloud around apex of second vein; fore femur with strong bristles on ventral surface .....*rufa* (Panzer)



Figs. 21-30.—Male genitalia of various species (all measurements in mm; figures modified from Steyskal, 1950, 1954d and 1959). 21.—*Dictya pictipes* (Loew). 22.—*D. borealis* Curran. 23.—*D. stricta* Steyskal. 24.—*D. expansa* Steyskal. 25.—*D. incisa* Curran. 26.—*D. montana* Steyskal. 27.—*Sepedon neili* Steyskal. 28.—*S. lignator* Steyskal. 29.—*Tetanocera plebeia* Loew. 30.—*T. nanciae* Brimley.

Wing without brownish cloud around apex of second vein (Fig. 1); fore femur without strong bristles on ventral surface ..... *connexa* Steyskal

Genus *Limnia* Desvoidy

1. Brown costal border of wing interrupted by clear spots (Fig. 5) ..... *boscii sparsa* (Loew)
   Brown costal border not interrupted by clear spots (Fig. 4) 2
2. Second antennal segment much longer than third segment and with several long bristles above (Fig. 19) ..... *pubescens* (Day)
   Second antennal segment only slightly longer than third segment, usually only bisetose above (Fig. 20) 3
3. Posterior cross vein nearly perpendicular; prescutellar bristles vestigial or wanting 4
   Posterior cross vein distinctly sinuate; prescutellar bristles more or less well-developed 5
4. Wing with brown costal border ending at apex of third vein; mesonotal vittae faint ..... *costalis brevicostalis* Melander
   Wing with brown costal border continuing to or beyond apex of fourth vein; mesonotal vittae conspicuous ..... *costalis vittata* Melander
5. Front wider than long; wing spots nearly hyaline; male with posterior surface of hind femora strongly spinose ..... *saratogensis armipes* Melander
   Front square or longer than wide; male with posterior surface of hind femora weakly spinose ..... *saratogensis saratogensis* (Fitch)

Genus *Renocera* Hendel

1. Humeral bristle present; prosternum with setae; one fronto-orbital bristle ..... *cyathiformis* Melander
   Humeral bristle lacking; prosternum bare; two fronto-orbital bristles ..... *johnsoni* Cresson

Genus *Sepedon* Latreille

1. Supraspiracular convexity of metathorax bare ..... *fuscipennis* Loew
   Supraspiracular convexity with numerous black hairs 2
2. Middle of face bare, only parafacies with black hair ..... *spinipes americana* Steyskal
   Middle of face with scattered black hairs 3
3. Second antennal segment distinctly compressed; body over 7.5 mm in length ..... *praemiosa* Giglio-Tos
   Second antennal segment slender, less compressed; body less than 6.0 mm in length 4
4. Hind femur of male with deep indentation on ventral surface, hind femur of female without indentation; abdomen brown, usually with only slight indication of bluish color 5
   Hind femora of both sexes without indentation on ventral surface, abdomen often with distinct bluish reflection on dorsal surface 8
5. Frons with only very slight indication of black parafrontal spots; basimedian prong on ventral surface of hind femur of male distinctly bifid (known only from California) ..... *bifida* Steyskal
   Frons with densely black parafrontal spots 6
6. Subbasal prong on ventral surface of hind femur of male much closer to basimedian prong than to base of femur (Fig. 15); orbito-antennal spots of both sexes with brownish borders ..... *anchista* Steyskal
   Subbasal prong on hind femur of male about equidistant from base of femur to basimedian prong; orbito-antennal spots of both sexes large, wholly black 7

7. Parafrontal black spots very large, reaching nearly to vertex; length of subbasal prong on hind femur of male less than one-half width of femur, (known only from Snoqualmie Pass, Washington) ..... *melanderi* Steyskal
Parafrontal spots small, not extending halfway to vertex, length of subbasal prong more than one-half width of hind femur (Fig. 16) ..... *armipes* Loew
8. Pruinose median stripe on face blunt at apex, not reaching oral margin; body dark colored with distinct bluish reflection; prosternum with five or fewer hairs on each side ..... *borealis* Steyskal
Pruinose median stripe on face extending as a point to oral margin; body usually browner; prosternum with more than five hairs on each side 9
9. Male genitalia as figured (Fig. 28) ..... *lignator* Steyskal
Male genitalia as figured (Fig. 27) ..... *neili* Steyskal

Genus *Tetanocera* Duméril

1. Posterior side of middle femur with more than one bristle toward apex, usually three 2
Posterior side of middle femur with only one bristle or completely lacking bristles near apex 3
2. Prosternum with setae ..... *robusta* Loew
Prosternum bare ..... *annae* Steyskal
3. Posterior side of middle femur with single bristle near apex 4
Posterior side of middle femur without bristles near apex 8
4. Hairs on parafacies extending well above midpoint between lower margin of eye and base of antenna (Fig. 9) black orbito-antennal spot present 5
Parafacial hairs not reaching midpoint between lower margin of eyes and antennal bases (Fig. 10) 6
5. Fourth vein with one or more stump veins ..... *vicina* Macquart
Fourth vein without stump veins; male genitalia as figured (Fig. 30) ..... *nanciae* Brimley
6. Aristal hairs very dense and black; orbito-antennal spot usually large and black ..... *obtusifibula* Melander
Aristal hairs scattered and somewhat sparse; orbito-antennal spot usually faint or lacking 7
7. Bristles on posterior surface of fore femur usually at least as long as width of femur ..... *mesopora* Steyskal
Bristles on posterior surface of fore femur short; about one-half width of femur ..... *latifibula* Frey
8. Hind femur with a posterodorsal bristle opposite preapical bristle (Fig. 13) 9
Hind femur without posterodorsal bristle 11
9. Fourth vein with stump veins ..... *rotundicornis* Loew
Fourth vein without stump veins 10
10. Parafrontal stripes broad and strongly shining (Fig. 8); second posterior cell with dark cloud; medifacies of female shining; male genitalia as figured (Fig. 29) ..... *plebeia* Loew
Parafrontal stripes narrow; second posterior cell hyaline; medifacies of female pruinose ..... *montana* Day
11. Wing membrane with numerous brown spots (Fig. 3) ..... *valida* Loew
Wings without brown spots in membrane 12
12. Frons largely shining, midfrontal stripe broadly triangular ..... *unicolor* Loew
Frons mostly dull, midfrontal stripe narrow, parallel-sided 13
13. Anterior margin of front slightly raised and strongly shining, connecting midfrontal and parafrontal stripes anteriorly ..... *silvatica* Meigen

Anterior margin of front flattened, not shining 14
14. Parafrontal stripes broad, strongly shining (Fig. 8); second posterior cell usually with dark cloud on membrane; medifacies of female shining; male genitalia as figured (Fig. 29) ..... *plebeia* Loew
Parafrontal stripes narrow (Fig. 7); medifacies of female pruinose 15
15. Midfrontal stripe narrow, not reaching anterior margin of frons (Fig. 7); wings without stump veins ..... *ferruginea* Fallén
Midfrontal stripe broader, clearly reaching anterior margin of frons 16
16. Aristal hairs dense and black, third antennal segment distinctly concave dorsally (Fig. 17) ..... *soror* Melander
Aristal hairs sparse, paler, third antennal segment usually not concave dorsally 17
17. Blackish orbito-antennal spot present; wings without stump veins ..... *spirifera* Melander
Orbito-antennal spot absent; wings with stump veins on fouth vein ..... *nigricosta* Rondani

DISTRIBUTION RECORDS

Most of the distributional data presented are based on specimens examined by the author, but in some instances significant records available in the literature are included. If a year is not listed, the specimens were collected during 1959. Unless otherwise indicated, the records were obtained by the author. For Idaho, all collection data are given, but for the other northwestern states and provinces only the place of collection is listed.

SCIOMYZINAE

Atrichomelina pubera (Loew).—Foote *et al.* (1960) state that the larval stages are associated with pulmonate aquatic snails that have been stranded by a receding water level. At Robinson's Lake large numbers of larvae were discovered in *Physa gyrina* snails that were exposed on the wet mud. IDAHO: Robinson Lake, September 28, 1959, May 11; 5 miles N. of Troy, September 6, 1958; 2 miles E. of Spencer, July 15, 1956 (W. F. Barr); Star Lake, July 4 (D. L. Bishop); 10 miles W. of Mack's Inn, July 17. UTAH: Dry Lake. WASHINGTON: Pullman. OREGON: near Corvallis, Klamath Falls, Salem-Albany, Philomath, Newport. ALBERTA: Medicine Hat.

Sciomyza dryomyzina Zetterstedt.—A single specimen collected on July 22 in the Stanley Basin, 10 miles N. of Galena Summit constitutes the only record for the state. In Alaska, Berg (1953) reared an adult from a larva found in the marsh-inhabiting snail *Oxyloma decampi gouldi* (Tyron). At the collecting station in Stanley Basin, *Oxyloma* snails are abundant. Apparently the only previous record for the species in North America is Alaska (Steyskal, 1954).

Sciomyza simplex Fallén.—Foote (1959) reared adults from larvae feeding in *Oxyloma* snails. In Idaho the species was found only in marshes that contained large populations of *Oxyloma*. IDAHO: Bonners Ferry, August 13, 1958; Bancroft, August 3, 1958; Swan Lake, July 18; Bear Lake, July 10. MONTANA: Hill Co. UTAH: Dry Lake. OREGON: Klamath Falls. ALBERTA: Medicine Hat, Cooking Lake. BRITISH COLUMBIA: Agassiz, Nicola, Kamloops.

Pherbellia albocostata (Fallén).—Not yet recorded from Idaho. WYOMING: Jenny Lake in Great Teton National Park. ALBERTA: Banff.

Pherbellia griseola (Fallén).—Common in marshes having a water level that gradually recedes as summer advances. IDAHO: Copeland, June 6; 3 miles S. of Worley; Robinson Lake, May 11; Vassar Meadows, June 6; 3 miles S. of Deary, May 14; Donnelly, August 30, 1952 (W. F. Barr). UTAH: Logan Canyon.

Pherbellia grisescens (Meigen).—Common, but rarely abundant, in open marshes throughout the state. IDAHO: Robinson Lake, late August and early September, 1958, May 11; Hazelton, September 7, 1954 (W. F. Barr); 4 miles E. of Shoshone, May 22; 10 miles W. of Mack's Inn, July 16; Henry's Lake, July 17. UTAH: Snowville, Hooper, Tremonton, Logan, Elberta, Burbank. WASHINGTON: White Bluffs, O'Sullivan Dam. OREGON: Butte Falls. ALBERTA: Orion, Medicine Hat.

Pherbellia nana (Fallén).—Common to abundant in open marshes throughout the state. IDAHO: Three miles S. of Worley, June 2; Robinson Lake, late August, 1958; Bruneau, June 25; 15 miles S. of Fairfield, May 21; 4 miles E. of Shoshone, May 22; 14 miles N. of Mackay, May 31 (W. F. Barr); Salmon, May 25, 2 miles E. of Spencer, July 15, 1956 (W. F. Barr); 10 miles W. of Mack's Inn, July 17; Swan Lake, July 18; Bear Lake, July 10. UTAH: Ogden, Richmond, Huntsville, Providence, Pleasant Grove, Brigham, Nephi, Hooper, Woodscross, Bluffdale, Logan Canyon, Cotton. WASHINGTON: White Bluffs, Willow Creek near Lagrosse. OREGON: Pringle Falls W. of Lapine, Prospect, Prineville, 20 miles S. of Bend, Seappoose, 12 miles S. of Corvallis, near Ukiah. ALBERTA: Edmonton.

Pherbellia obtusa (Fallén).—Recorded from Bear Lake on July 19 when approximately 60 adults were taken during a two-hour search of the marsh. ALBERTA: Red Deer.

Pherbellia schoenherri (Fallén).—Occasionally common in unshaded marshes throughout the state. IDAHO: 8 miles N. of Sandpoint, June 1; 3 miles S. of Worley, July 8; Troy, September 6, 1958; 4 miles E. of Genesee, May 13; Dixie, April 17 (W. F. Barr); Hagerman, April 12; 2 miles W. of Gannett, May 22; 14 miles N. of Mackay, May 31 (W. F. Barr). WYOMING: Jenny Lake in Great Teton National Park. UTAH: Logan Canyon. OREGON: 27 miles E. of Prineville, Summit Prairie. ALBERTA: Medicine Hat, Cooking Lake. BRITISH COLUMBIA: Sorenson Lake near Caribou.

Pherbellia tenuipes (Loew).—Not yet discovered in Idaho, but reported from Terrace, British Columbia, by Steyskal (personal communication).

Pherbellia vitalis (Cresson).—Abundant throughout the state in marshes having a water level that recedes gradually during the summer. IDAHO: Copeland, June 1; 8 miles N. of Sandpoint, June 1; 3 miles S. of Worley, May 12, June 2; Moscow, April 8, 1936 (R. E. Miller), May 7; Robinson Lake, late August, 1958, May 11; Vassar Meadows, May 6; 3 miles S. of Deary, May 14; 12 miles S. of Pollock, June 26; Bruneau, June 25; Hagerman, June 20; 15 miles S. of Fairfield, May 21; Hill City, August 27, 1926 (R. W. Haegele); near Craters of Moon National Monument, July 30, 1958 (A. R. Gittins); 10 miles W. of Mack's Inn, July 17; Swan Lake, July 18; Henry's Lake, July 17; Bear Lake, July 10. UTAH: Kanesville, Dry Lake, Hooper, West Jordan, Joseph, Benson, Slaterville. WASHINGTON: Hanford Works, Lind Lake, Paha, Field Springs State Park, Wawawai, Pullman, White Bluffs, O'Sullivan Dam. OREGON: Butte Falls, Cold Springs, St. Helens.

Pteromicra apicata (Loew.)—Not yet discovered in Idaho, but reported from Washington by Melander (1920).

Pteromicra leucothrix Melander.—Not yet discovered in Idaho, but reported from Orcas Island, Washington by Melander (1920).

Pteromicra melanothrix Melander.—Not yet discovered in Idaho, but reported from Yellowstone Lake, Wyoming by Melander (1920).

Pteromicra nigrimana (Meigen).—Common to abundant in grass-sedge marshes that become partially dry as summer advances. IDAHO: Bonners Ferry, early September, 1958; 12 miles N. of Granite, July 8; 4 miles E. of Shoshone, June 19; 14 miles N. of Mackay, May 31 (W. F. Barr); Swan Lake, July 18, Bear Lake, July 19. WYOMING: Yellowstone Lake. WASHINGTON: Pullman.

Pteromicra pectorosa (Hendel).—Not yet discovered in Idaho, but reported from the extreme northwestern corner of California by Steyskal (1957).

Pteromicra perissa Steyskal.—Not yet discovered in Idaho, but reported from Buffalo Peaks Area in Chaffee and Parks Counties, Colorado, by Steyskal (1957).

Colobaea americana Steyskal.—Not yet discovered in Idaho, but reported from Aweme, Manitoba, by Steyskal (1954a).

TETANOCERINAE

Antichaeta melanosoma Melander.—A single male taken along margins of easternmost pond at Copeland on July 1 constitutes the only Idaho record. Apparently this is a new record for the Pacific Northwest as all previously known specimens were taken in the northeastern states.

Antichaeta robiginosa Melander.—Not yet discovered in Idaho. OREGON: Roberts. The holotype was collected at Three Forks, Montana (Melander, 1920).

Antichaeta testacea Melander.—Fairly common in marshes during late May and June. IDAHO: 4 miles E. of Shoshone, May 22; Gannet, May 22; Elba-Basin Pass, June 22. UTAH: Parowan, Midvale, Payson. Holotype collected in Gallatin County, Montana (Melander, 1920).

Antichaeta sp. A.—IDAHO: Eight miles N. of Sandpoint, June 1.

Dictya borealis Curran.—Not yet discovered in Idaho, but reported from Manitoba and Saskatchewan by Steyskal (1954d).

Dictya expansa Steyskal.—In Alaska, Berg (1953) reared larvae on aquatic pulmonate snails. In Idaho, the species was common to abundant in the more permanent marshes that had large populations of *Physa* sp. and *Lymnaea palustris*. IDAHO: Bonners Ferry, August 18, 1958; Hauser Lake, May 22 (H. W. Homan); 3 miles S. of Worley, May 26, July 8; Robinson Lake, September 15, 25, 1958; Spaulding, May 17, 1954 (W. F. Barr); 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, May 25; Roberts, August 1, 1958. WASHINGTON: Pullman, Ilwaco, White Bluffs. OREGON: Cold Springs.

Dictya incisa Curran.—Not yet discovered in Idaho, but reported from Utah (Leeds, Mirror Lake, St. George, Spanish Fork, Uintah Mts.) and Washington (Yakima) by Steyskal (1954d).

Dictya montana Steyskal.—Common to abundant in permanent marshes throughout the state. IDAHO: Eight miles N. of Sandpoint, July 8; Kellogg, August 14, 1926 (R. W. Haegele); Robinson Lake, August 14, September 6, 1958, September 25; Vassar Meadows, May 6; Pierce, August 4, 1926 (R. W. Haegele); Dixie, April 17; Hagerman, May 23; 4 miles E. of Shoshone, May 22, June 1, July 10 (D. L. Bishop); Clover, August 25, 1953 (A. R. Gittins); Elba-Basin Pass, June 26; 2 miles W. of Gannet, May 22, July 22; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Fish Haven, May 21, 1949 (G. F. Knowlton). UTAH: Ogden, Brigham, Benson, Logan, Logan Canyon, Payson, Slaterville, Hooper, Riverdale, Eden, Farmington, Duchesne.

WASHINGTON: Pullman, O'Sullivan Dam, Anacortes. OREGON: Butte Falls, Deschutes River near Redmond, 10 miles SE. of Prineville, Odell Lake, near Corvallis, 10 miles N. of Seneca, Medford.

Dictya pictipes (Loew).—Not yet discovered in Idaho, but reported from Ravalli County, Montana by Steyskal (1954d).

Dictya stricta Steyskal.—Three specimens from 20 miles S. of Salmon and five specimens from two miles N. of Salmon taken on May 25 constitute the Idaho records. All specimens were taken in wooded situations (mostly willows, alders, and cottonwoods) with some standing water present. MONTANA: Three Forks. UTAH: Richmond.

Dictya umbroides Curran.—Not yet discovered in Idaho, but reported from northern British Columbia by Steyskal (1954d).

Dictyacium firmum Steyskal.—IDAHO: Priest River Forest Experiment Station, August 14, 1958 (A. R. Gittins); Craigmont, July 22, 1952 (W. F. Barr).

Hedria mixta Steyskal.—Not yet discovered in Idaho, but reported from Alberta (Wabamun, Nordegg) and Saskatchewan (Waskesiu Lake) by Steyskal (1954a).

Hedroneura connexa Steyskal.—Fairly common in the more permanent marshes across the southern part of the state. IDAHO: Donnelly, August 12, 1952 (S. E. Knapp); Dixie, June 20, 1953 (W. F. Barr), April 12, 19; Rock Creek Ranger Station, Sawtooth National Forest, June 20; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Bancroft, August 3, 1958. UTAH: Logan Canyon, Wasatch. OREGON: 10 miles S. of Corvallis, 10 miles N. of Seneca. ALBERTA: Banff.

Hedroneura rufa Panzer.—In Alaska, Berg (1953) discovered that the larval stages are predaceous on aquatic pumonate snails. In Idaho, third-instar larvae were found at the north end of Robinson Lake during late August, 1958. IDAHO: Copeland, July 1; Bonners Ferry, August 13, 1958; 8 miles N. of Sandpoint, July 8; Robinson Lake, late August, 1958, March 3, May 11, June 1; 3 miles W. of Parma, June 19 (H. W. Homan); Dixie, June 20, 1953 (W. F. Barr), April 17; Fairfield, August 27, 1926 (R. W. Haegele); Gannet, May 22, July 22; Hagerman, May 23, June 20; Bancroft, August 3, 1958; Bear Lake, July 19. MONTANA: Gallatin Co. UTAH: Taylor, Riverdale, Syracuse, Greendale, Corinne, Harper, Far West, Logan, Hooper, Charleston, Garden City, College Ward, Brigham, Ogden. ALBERTA: Edmonton, Wabamun. BRITISH COLUMBIA: Westwick Lake, Kamloops, Quesnel, Nicola.

Hoplodictya spinicornis (Loew).—Fairly common in more permanent marshes in the southern counties of the state. IDAHO: Fruitland, June 8, 1935 (B. F. Coon); 3 miles W. of Parma, June 19 (H. W. Homan); Hot Creek Falls, April 12; Hagerman, April 12. WASHINGTON: O'Sullivan Dam.

Limnia boscii sparsa Loew.—IDAHO: 12 miles N. of Granite, July 8; Elk River, July 4. MONTANA: Glacier Park. Melander (1920) reports this species from Washington.

Limnia costalis brevicostalis Melander.—The type material came from Avon, Idaho (Melander, 1920).

Limnia costalis vittata Melander.—Melander (1920) reports specimens from Montana, Idaho and Washington.

Limnia pubescens (Day).—IDAHO: Moscow, August 8, 1936 (B. F. Coon); Robinson Lake, August 14, September 6, 1958; Lewiston Grade, July 2, 1949 (M. T. James); Kendrick, August 26, 1951 (W. F. Barr). UTAH: Brigham,

Logan. WASHINGTON: Albion, Pullman. OREGON: Portland, Phoenix, Monroe, near Corvallis. ALBERTA: Victoria.

Limnia saratogensis armipes Melander.—The type material came from Olga, Washington (Melander, 1920).

Limnia s. saratogensis (Fitch).—IDAHO: 12 miles N. of Granite, July 8; Gannet, July 22; Fish Haven, July 6, 1951 (G. F. Knowlton). UTAH: Logan, Providence, Salt Lake City, Newton, Lakota, Leeds. WASHINGTON: San Juan Island, Ocean Park. OREGON: Corvallis, Charleston, Spanaway Lake. ALBERTA: Edmonton, Fawcett, Medicine Hat. BRITISH COLUMBIA: Victoria, Chilcotin, Winslow, Kamloops, Goldstream.

Renocera cyathiformis Melander.—IDAHO: 8 miles N. of Sandpoint, June 1, July 8; Elk River, July 4; Stanley Basin, July 22. WASHINGTON: Holotype collected on Orcas Island (Melander, 1920).

Renocera johnsoni Cresson.—IDAHO: Priest River Forest Experiment Station, June 2; Stanley Basin, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); Henry's Lake, July 17. UTAH: Monte Cristo. BRITISH COLUMBIA: Paratype collected at Bear Lake (Cresson, 1920).

Sepedon anchista Steyskal.—Four specimens collected July 19 at Bear Lake constitute the only Idaho records. Steyskal (1956) reports it from Montana.

Sepedon armipes Loew.—Abundant in permanent marshes throughout the state. IDAHO: Priest River Forest Experiment Station, June 2; Bonners Ferry, August 11, 1926 (R. W. Haegele); 8 miles N. of Sandpoint, June 1, July 8; Hauser Lake, May 22 (H. W. Homan); Robinson Lake, September 25; Troy, April 5, 1958; Roswell, July 27 (H. W. Homan); 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, June 25; Hot Creek Falls, June 27, 1953 (W. F. Barr), April 12; Dixie, June 20, 1953 (W. F. Barr), April 17, June 19; Little Camas Reservoir, June 29 (W. F. Barr); Hagerman, May 23, June 20; Hazelton, September 4, 7, 1954 (W. F. Barr); 4 miles E. of Shoshone, May 22, June 19, July 10; Gannet, May 22, July 22; Stanley Basin, July 22; Salmon, May 25; 2 miles N. of Gilmore, July 24 (H. C. Manis); Massacre Rocks, July 28, 1958 (A. R. Gittins); Bancroft, August 3, 1958. MONTANA: Three Forks, Gallatin Co., Ravalli Co. WYOMING: Jenny Lake in Great Teton National Park. UTAH: Orem, Providence, Brigham, Logan Canyon, Laketown, Ogden, Eden, Mendon, Hooper, Delta, Leeton, Myton, Vernal, Kanesville, Marysvale, Duchesne, Plain City, Lyman, Midvale, Salina Canyon, Spring Run. WASHINGTON: Willow Creek near LaCrosse, O'Sullivan Dam, Coulee. OREGON: Cold Springs, near Prospect, Butte Falls, Minam, 10 miles N. of Seneca, Tumalo Reservoir. ALBERTA: Edmonton, Medicine Hat, Cooking Lake. BRITISH COLUMBIA: Oliver, Kamloops.

Sepedon borealis Steyskal.—Locally common in the more permanent marshes. IDAHO: Priest River Experiment Station, June 2; Dixie, July 31, 1951, April 17 (W. F. Barr), June 19; Gannet, July 22; Stanley Basin, July 22. UTAH: Logan Canyon. OREGON: Corvallis. BRITISH COLUMBIA: Peace River at Fort St. John.

Sepedon fuscipennis Loew.—Abundant in more permanent marshes in northern counties. Not yet recorded from southern and eastern counties where it is apparently replaced by *Sepedon praemiosa*. IDAHO: Kalispel Bay on Priest Lake, July 7; 4 miles S. of Coeur d'Alene, July 14; Granite Lake, June 1; near Westmond, July 8; 3 miles S. of Worley, June 2; Rocky Point on Lake Chatcolet, September 7, 1953 (M. T. James); Robinson Lake, October 12, 1950 (J. K. Vaughn), late August, 1958, May 11; Vassar Meadows, May 6. MONTANA: Ravalli Co. WASHINGTON: Anacortes, Orcas Island, Fort Lewis, Tenino. ORE-

GON: Klamath Falls, 12 miles S. of Corvallis. ALBERTA: Lethbridge, Wabamun, Edmonton. BRITISH COLUMBIA: Agassiz, Haney, Quesnel.

Sepedon lignator Steyskal.—Reported by Steyskal (1959) from Wyoming (Yellowstone Park), Montana (Glacier Park), Alberta (Banff), and British Columbia (Oliver).

Sepedon melanderi Steyskal.—Known only from Snoqualmie Pass, Washington (Steyskal, 1950).

Sepedon neili Steyskal.—IDAHO: Granite Lake, July 2; 3 miles S. of Worley, June 2. Previously this species was known only from the eastern states extending west to Kansas (Steyskal, 1950).

Sepedon praemiosa Giglio-Tos.—Abundant in permanent marshes and in marshy margins of lakes throughout the state. IDAHO: Four miles S. of Coeur d'Alene, July 14; Robinson Lake, October 12, 1950 (J. K. Vaughn), September 6, 1958, May 11; 12 miles S. of Pollock, June 26; 3 miles W. of Parma, June 19 (H. W. Homan); Bruneau, June 25; Dixie, April 17, June 20 (W. F. Barr); Little Camas Reservoir, May 29 (W. F. Barr); Hagerman, April 12, May 23 (R. W. Portman); Rock Creek Ranger Station, Sawtooth National Forest, June 20; 4 miles E. of Shoshone, May 23, June 19; Star Lake, July 4 (D. L. Bishop); Hazelton, August 18, 1954 (A. R. Gittins); Gannet, July 22; 2 miles N. of Gilmore, July 24 (H. C. Manis); 5 miles N. of Roberts, July 29, 1958 (A. R. Gittins); Bear Lake, July 19. UTAH: Woodscross, Iron Springs, Moab, Harper, Vernal, Green River, Howell, Eureka, Penrose, Logan Canyon, Ogden, Zion Canyon, Randolph, Uinta, Blue Creek, Emery, Syracuse, Hooper, Kamas, Hyde Park, Geneva, Leeds, Brigham, Wellsville, Lehi, Hansville, Amalga, Pahvant. WASHINGTON: Richland, White Bluffs, Pullman, Marietta, O'Sullivan Dam. OREGON: Klamath Co. Fish Hatchery, Cold Springs. ALBERTA: Medicine Hat, Lethbridge.

Sepedon spinipes americana Steyskal.—IDAHO: Bonners Ferry, August 13, 1958; Bear Lake, July 19. UTAH: Wellsville. OREGON: Corvallis. ALBERTA: Wabamun, Fawcett, Clymont.

Tetanocera annae Steyskal.—Not yet discovered in Idaho. BRITISH COLUMBIA: Salmon Arm. Steyskal (1959) records the species from Agassiz, B. C.

Tetanocera ferruginea Fallén.—Berg (1953) reported that the larval stages are predators on aquatic pulmonate snails. In Idaho, a larva was found feeding on a *Lymnaea palustris* snail at the marsh east of Shoshone on May 22. IDAHO: Eleven miles E. of Rogerson, July 20, 1952 (W. F. Barr); Hagerman, May 23; 4 miles E. of Shoshone, May 22, June 19; Gannet, May 22; Mackay, July 7, 1926 (R. W. Haegele); Salmon, May 25; Bancroft, August 3, 1958. UTAH: Salt Lake City, Wellsville. OREGON: Buena Vista, 19 miles N. of Frenchglen. BRITISH COLUMBIA: Prince George, Kamloops, Agassiz.

Tetanocera latifibula Frey (= *hespera* Steyskal).—IDAHO: Dixie, June 19; Stanley Basin, July 22; Swan Lake, July 18; Bear Lake, July 19. UTAH: Pahvent. ALBERTA: Edmonton. BRITISH COLUMBIA: Quesnel, Kamloops, Prospect Lake.

Tetanocera mesopora Steyskal.—IDAHO: Henry's Lake, July 17; Swan Lake, July 18. UTAH: College Ward. ALBERTA: Edmonton.

Tetanocera montana Day.—IDAHO: 10 miles S. of Sandpoint, July 8; Swan Lake, July 18. MONTANA: Fortine. ALBERTA: Tofield, Wabamun, Nordegg, Banff. BRITISH COLUMBIA: Kamloops.

Tetanocera nanciae Brimley.—Abundant in marshes and swales throughout the state. IDAHO: Westmond, July 8; Robinson Lake, September 15, 1958, June

10; Laird Park, June 24, 1949 (M. T. James); Kendrick, August 26, 1951 (W. F. Barr); Elk River, July 4; 12 miles S. of Pollock, May 30; Hot Creek Falls, July 12, 1952 (W. F. Barr); Bruneau, June 25; Dixie, June 20, 1953 (W. F. Barr), June 19; Rock Creek Ranger Station, Sawtooth National Forest, July 19, 1952 (W. F. Barr); 4 miles E. of Shoshone, May 22, June 19, June 29 (D. L. Bishop); Dietrich, July 9 (D. L. Bishop); Gannet, July 22; Stanley, August 6, 1950 (R. W. Portman); Challis, June 23, 1952 (E. I. Schlinger); near Mackay, July 30, 1958 (A. R. Gittins); 2 miles N. of Gilmore, July 24 (H. C. Manis); Arco, August 8, 1958; Massacre Rocks, July 28, 1958; Kilgore, July 15, 1956 (W. F. Barr); Henry's Lake, July 17; Sugar City, August 10, 1940 (W. E. Shull); near Aberdeen, July 8, 1957 (A. R. Gittins); Wayan, July 16, 1940 (W. E. Shull); Montpelier, July, 1951 (G. F. Knowlton). MONTANA: Lewistown, Sahara, Fortine. WYOMING: Yellowstone Park, Sheridan. UTAH: Logan, Kamas, Devil's Kitchen, Hyde Park, Marysvale, Laketown, Woodruff, Eden, Wahship, Payson, Mantua, Vernal, Promontory, Fairview, Garden City, Linden, Smithfield, Hooper, Plain City. WASHINGTON: Ocean Park, Pullman, N. Yakima, Johnson, Rainier National Forest, O'Sullivan Dam, Grand Coulee, near Spanaway, Spanaway Lake, Fort Lewis. OREGON: Klamath Falls, Minam, Redmond, near Prospect, Enterprise, 20 miles S. of Bend, Powell Butte, Tumalo Reservoir, 10 miles NE. of LaPine. ALBERTA: George Creek, Nordegg, Banff, Wabamun, Edmonton, Pincher, Cypress Hills, Medicine Hat. BRITISH COLUMBIA: Jesse Island, Kamloops, Quesnel, Vernon, Nicola, Smithers, Chilcotin, Agassiz, Prospect Lake.

Tetanocera nigricosta Rondani.—Not yet discovered in Idaho. ALBERTA: Edmonton, Fawcett, Wabamun, Wetaskiwin, Gull Lake. Melander (1920) records the species from Mt. Constitution, Washington.

Tetanocera obtusifibula Melander.—IDAHO: Near Moscow, May 30. Melander (1920) had type material from Worley, Idaho. WASHINGTON: Pullman, Chambers. OREGON: Nine miles N. of Brownsville, slough 10 miles S. of Corvallis.

Tetanocera oxia Steyskal.—Not yet discovered in Idaho. MONTANA: Three Forks. Steyskal (1959) records the species from Fawcett, Alberta.

Tetanocera plebeia Loew.—Fairly common, but local, in both permanent and vernal marshes throughout the state. IDAHO: Kalispel Bay on Priest Lake, July 7; 8 miles N. of Sandpoint, July 8; Westmond, July 8; Robinson Lake, September 10, 1958; Elk River, July 4; 12 miles S. of Pollock, May 10, June 26; Dixie, June 19; Stanley Basin, July 22; 4 miles E. of Shoshone, June 19; Declo, September 14, 1930 (F. Gillett). WYOMING: Yellowstone Park. UTAH: Newton, Henefore, Woodruff, Mt. Home, Logan, Kanab, Mt. Nebo. WASHINGTON: Walla Walla, Ilwaco. OREGON: Enterprise, near Prospect, Summit Prairie, Odell Lake, near Sisters. ALBERTA: Nordegg, Banff, Edmonton.

Tetanocera robusta Loew. — Abundant in the more permanent marshes throughout the state. IDAHO: Priest River Forest Experiment Station, June 1, Bonners Ferry, August 13, 1958; 8 miles N. of Sandpoint, June 1, July 8; Robinson Lake, late August, 1958; Kendrick, September 25; Spaulding, May 17, 1954 (W. F. Barr); Bruneau, June 25; Little Camas Reservoir, May 29 (W. F. Barr); Hagerman, June 20; 4 miles E. of Shoshone, June 29 (D. L. Bishop); Declo, September 14, 1930 (J. Gillett); Elba-Basin Pass, June 22; Stanley Basin, July 22; Hailey, July 28, 1956 (R. W. Portman); 2 miles N. of Gilmore, July 24 (H. C. Manis); Sugar City, July 21, 1926 (R. W. Haegele); Bancroft, August 3, 1958; Fish Haven, July 6, 1951 (G. F. Knowlton). MONTANA: Hamilton, Phillipsburg. UTAH: Newton, Midway, Benson, Heber, Logan, Hyrum, Milford, Lehi, Pahvant, Wallsburg, Wellsville, Randolph, Hooper, Valencia,

Plain City, Ogden. WASHINGTON: Pullman, Harrah, Ocean Park, Custer, Prosser. OREGON: Klamath Falls, Pringle Falls, Enterprise, Blue Mt. Hot Springs, 10 miles S. of Corvallis, Swim, near Strawberry Lake. ALBERTA: Nordegg, Winterburn, Gull Lake, Medicine Hat, Calgary. BRITISH COLUMBIA: Soda Creek, Kamloops.

Tetanocera rotundicornis Loew.—Berg (1953) reared adults from larvae found in the land snail *Oxyloma decampi gouldi*. In Idaho, the species was found only in those marshes containing large populations of *Oxyloma*. IDAHO: Eight miles N. of Sandpoint, July 8; Dixie, June 19; 4 miles E. of Shoshone, June 19, June 29 (D. L. Bishop); Gannet, July 22. OREGON: Klamath Falls. ALBERTA: Wabamun, Fawcett. BRITISH COLUMBIA: Chilcotin, Kamloops.

Tetanocera soror Melander.—IDAHO: Westmond, July 8; Moscow Mt., July 24, 1936 (B. F. Coon); Robinson Lake, August 14, September 6, 1958; Dixie, June 19. WASHINGTON: Chambers, Pullman, Orcas Island. OREGON: Summit Prairie, 10 miles S. of Corvallis, Corvallis.

Tetanocera silvatica Meigen.—Not yet discovered in Idaho. ALBERTA: Gull Lake, Wabamun, Mt. Athabasca. BRITISH COLUMBIA: Peace River at Fort St. John.

Tetanocera spirifera Melander.—Not yet discovered in Idaho. WYOMING: Jenny Lake in Great Teton National Park. Steyskal (1959) records the species from Alberta (Banff National Park) and British Columbia (Atlin).

Tetanocera unicolor Loew.—IDAHO: Bonners Ferry, August 11, 1926 (R. W. Haegele); 8 miles N. of Sandpoint, June 1, July 8; Gannet, July 22; Stanley Basin, July 22. MONTANA: Three Forks.

Tetanocera valida Loew.—Not yet discovered in Idaho. UTAH: Logan. ALBERTA: Edmonton, Vermillion, Medicine Hat, Gorge Creek. BRITISH COLUMBIA: Chilcotin.

Tetanocera vicina Macquart.—IDAHO: Eight miles N. of Sandpoint, July 8; Rocky Point on Lake Chatcolet, July 1, 1953 (M. T. James); Robinson Lake, October 1, 1958; Elk River, July 4; 3 miles W. of Parma, June 19 (H. W. Homan); Dixie, June 19; Bear Creek Camp, 10 miles N. of Leslie, July 10, 1956 (W. F. Barr); Henry's Lake, July 17. WYOMING: Yellowstone Park. UTAH: Miner's Peak. WASHINGTON: Ocean Park, Marietta, Pullman, Orcas Island. OREGON: Butte Falls, Sheep Creek, Minam, Corvallis, near Prospect, north of LaPine.

Trypetoptera canadensis (Macquart).—Not yet discovered in Idaho. MONTANA: Sahara. UTAH: Logan, Wellsville, Nible, Brigham, Ogden, Smithfield. BRITISH COLUMBIA: Langley, Jesse Island, Saanich District, Victoria.

REFERENCES

BERG, C. O. 1953. Sciomyzid larvae (Diptera) that feed on snails. *J. Parasitol.*, **39**(6):630-636.

———, B. A. FOOTE, AND S. E. NEFF. 1959. Evolution of predator-prey relationships in snail-killing sciomyzid larvae (Diptera). *Bull. Am. Malacol. Union*, **25**:10-13.

CARTER, H. G. 1941. Climate of Idaho. *In* Climate and Man. 1941 Yearbook of Agriculture. U.S.D.A. 1248 pp.

CRESSON, E. T., JR. 1920. A revision of the nearctic Sciomyzidae (Diptera, Acalyptratae). *Trans. Am. Entomol. Soc.*, **66**:27-89.

DICE, L. R. 1943. *The Biotic Provinces of North America*. Univ. of Michigan Press, Ann Arbor. 78 pp., 1 map.

FENNEMAN, N. M. 1931. *Physiography of Western United States.* McGraw-Hill, New York. 534 pp., 173 figs., 1 pocket map.

FOOTE, B. A. 1959. Biology and life history of the snail-killing flies belonging to the genus *Sciomyza* Fallén (Diptera, Sciomyzidae). *Ann. Entomol. Soc. Am.*, **52**(1):31-43.

———, S. E. NEFF, AND C. O. BERG. 1960. Biology and immature stages of *Atrichomelina pubera* (Diptera, Sciomyzidae). *Ibid.*, **53**(2):192-199.

MASON, H. L. 1957. *A Flora of the Marshes of California.* Univ. of California Press, Berkeley. 878 pp.

MELANDER, A. L. 1920. Review of the nearctic Sciomyzidae. *Ann. Entomol. Soc. Am.*, **13**(3):305-332.

STEYSKAL, G. C. 1950. The genus *Sepedon* Latreille in the Americas (Diptera: Sciomyzidae). *Wassman J. Biol.*, **8**(3):271-297.

———1954a. *Colobaea* and *Hedria*, two genera of Sciomyzidae new to America (Diptera: Acalyptratae). *Can. Entomol.*, **86**(2):60-65.

1954b. The genus *Pteromicra* Lioy (Diptera, Sciomyzidae) with especial reference to the North American species. *Papers Mich. Acad. Sci.*, **39**: 257-269.

———1954c. The Sciomyzidae of Alaska (Diptera). *Proc. Entomol. Soc. Wash.*, **56**(2):54-71.

———1954d. The American species of the genus *Dictya* Meigen. *Ann. Entomol. Soc. Am.*, **47**(3):511-539.

———1956. New species and taxonomic notes in the family Sciomyzidae (Diptera: Acalyptratae). *Papers Mich. Acad. Sci.*, **41**:73-87.

———1957. A new species of the genus *Pteromicra* associated with snails (Diptera, Sciomyzidae). *Proc. Entomol. Soc. Wash.*, **59**(6):271-272.

———1959. The American species of the genus *Tetanocera* Duméril (Diptera). *Papers. Mich. Acad. Sci.*, **44**:55-91.

Investigations in the Life History of the Common Coturnix

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ABSTRACT: A compilation of the known life history data of *Coturnix coturnix* is presented. Topics include description of juvenal and adult plumage, weights and linear measurements. Voice, habitat and distribution are considered as well as aspects of reproduction. Decimating factors, rate of survival, food and behavior are also considered.

Introduction

The purpose of this paper is to summarize present knowledge concerning the life history of the quail *Coturnix coturnix*. The summary is based on a review of literature and on personal experience of the investigator in the laboratory and game farm. *C. coturnix* is a small, chubby, tailless, cinnamon-colored, terrestrial galliform introduced into North America from Japan during the late 1950's. It is 7 to 8½ inches in length. *Coturnix* now found in North America were stocked from game-farm propagated flocks of the subspecies *C. coturnix japonica*. It is extremely variable and adaptable in many aspects of its biology; probably an evolutionarily unstablized form with many accelerated and merostatic growth characters (Wetherbee, 1959a).

Description

Adult Male

Nuptial Plumage

Head.—Median stripe and superciliary line white; forehead, crown and nape black edged with brownish red; bill galliform but not robust, blackish brown to black, iris buffy brown ("yellow in old male birds," Montagu, 1831, probably in error); face and throat light brownish red. Nostrils slit-like, covered by an oblong operculum. Chin and throat with rounded feathers variable in tone, brownish red, perhaps darker brownish red with age, sometimes with black "anchor" mark (typical of the nominate race) consisting of blackish brown band descending from ear-coverts and terminating in throat patch; apparently most common after the second year.

Upper parts.—Large cinnamon feathers with few pale gray bars edged with black and with broad medial cream stripes.

Under parts.—Light cinnamon to light gray. Large pointed feathers of flank confluent with those of breast with white median stripe bordered by broad black and rufous edges.

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Tail.—Small, mostly concealed by coverts; rectrices 10 - 12 (Coues, 1903), coverts only 8 (Clark, 1918). Striped buffy brown, black and cream. Cloacal region swollen and reddish.

Wings.—Pointed due to long, curved tenth primary. Primary 10 as long or longer than 9 and emarginated on inner web; 9 and 8 emarginated on outer webs. Olive with about ten irregular cinnamon bars on outer webs of remiges; tertials buffy brown with several narrow pale gray bars edged with black. Greater coverts olive; lesser coverts brownish olive. Undersurface light gray; lesser under coverts white tinged with cinnamon.

Legs and feet.—Buffy yellow; without spurs; hind toe elevated.

Adult postnuptial molt.—Complete, extremely variable in time; June to January (Dementev and Gladkov, 1952), but usually in August (Witherby *et al.,* 1941); often absent in domestic stock (Kuroda, 1924). Stejneger (1885) reports shedding of claws; but this is probably pathological.

NON-NUPTIAL PLUMAGE

Feathers on chin and sides of throat long and lanceolate, generally whitish. Feathers on the lower parts rounded; some have blackish brown mark on medial throat suggesting "anchor" mark of nominate form (Kuroda, 1924). Juvenal distal primaries, retained in first non-nuptial plumage, have small sharp tips and coverts usually without white rachises; blunt primaries on second year birds and coverts usually with white rachises (David Lyon, personal communication). These covert markings are the reverse of age criteria for the Bobwhite (*Colinus virginianus*).

Prenuptial molt.—Contour feathers only, partial; February to April (Dementev and Gladkov, 1952), occasionally to May (Witherby *et al.,* 1941), especially for throat and flanks (Kuroda, 1924).

ADULT FEMALE

NUPTIAL PLUMAGE

Like male except feathers on chin and sides of throat long and pointed, much lighter cinnamon, usually margined on outer or both webs with rufous or black spots near tip without black median band. Postnuptial molt as in male.

NON-NUPTIAL PLUMAGE

As in nuptial plumage, pre-nuptial molt probably as in male.

COLOR PHASES

Albinism has been reported in females at the rate of "one in 70,000"; the eyes were pink and the feathers of the back and sides showed markings due to structure rather than pigment (Wint, 1957). "Blue" eyes were reported in albinos by Hachisuka (1931) who also reported that albinos lay white or pale bluish eggs with bluish markings. Shimakura (1940) described a simple, Mendelian, autosomal

recessive plumage character, "brown-splashed white." Incomplete melanism is reported by Dementev and Gladkov (1952); complete melanism, by Sturniolo (1913).

NATAL PLUMAGE

Relatively more dusky and striped than North American galliforms. Head tawny with black spot above culmen; medial stripe buffy brown bordered by black stripes; auricular patch black. Back and wings buffy brown with four blackish brown stripes on dorsum; tail and anterior border of wing blackish brown.

Natal down lost by abrasion; loss starts at 4 days and is completed last on head at about one month.

FIRST JUVENAL PLUMAGE

A few primaries are visible at hatching; all 10 are functional at 11 days at which time the chick can fly short distances. Ventral, femoral and humeral are visible at 4 days; capital, at 9 days. Plumage complete at 25 to 30 days (David Lyon, personal communication) except that primaries 9 and 10 are still sheathed at 21 and 42 days but clean at 7 weeks (Dementev and Gladkov, 1952). This plumage appears as adult female plumage except the cream medial streaks of spinal feathers are narrower and unsymmetrical (David Lyon, personal communication). Bill light brownish black.

First postjuvenal molt.—Contour feathers only, probably partial; breast, back and femoral feathers at 20 days of age to 50 days (David Lyon, personal communication), 26 to 42 days (Heinroth and Heinroth, 1928). Remiges: secondaries, centripetal, complete; primaries, centrifugal, incomplete (Dementev and Gladkov, 1952). First primary drops at 21 to 25 days; second, 22 to 27; third, 27 to 33; fourth, 33 to 36 (Edwards, ms.), 42 days (Dementev and Gladkov, 1952). David Lyon (personal communication) recorded first primary dropped at 22 to 29 days; second, 23 to 34; third, 27 to 39; fourth, 34 to 50; fifth, 34 to 75; sixth, 40 to 82, and seventh, 49 to 96 days. Wing molt becomes irregular and stops at sexual maturation (neoteny) which is variable in onset from of loss of fourth primary to loss of seventh or eighth primary (6 to 14 weeks).

SECOND JUVENAL PLUMAGE

Spinal feathers appear at 20 days, their light medial streaks are broad as in adult (David Lyon, personal communication). Sexes as in adult plumage with cinnamon on breast of male and female with speckled breast; a minority of specimens may not show sex dimorphism of plumage until first non-nuptial plumage (David Lyon, personal communication). The birds migrate with retained distal juvenal primaries.

Second post-juvenal molt.—Contour feathers only, complete at 11 to 13 weeks of age for July-hatched birds, 8 to 10 weeks for September-hatched birds (David Lyon, personal communication). Ac-

quisition of first non-nuptial plumage is accelerated for birds hatched late in the season, and as probably determined by photo-period of first half of October. Heinroth and Heinroth (1928) recorded 14 to 18 weeks, Stanford (1957), 20 to 22 weeks for this acquisition.

LINEAR MEASUREMENTS

Adult wing 91 - 104 mm, culmen 11.5 - 14.5 mm, tail 31-43 mm, tarsus 23.5 - 30.5 mm (120 from Japan, Kuroda, 1924); average wing 96 mm (27 from U.S.S.R., *C. c. japonica,* Dementev and Gladkov, 1952); body length 175 - 215 mm, wing-span 327 - 390 mm (34 from U.S.S.R., *C. c. coturnix,* Dementev and Gladkov, 1952); tarsus 17 mm at one week, 28 mm (maturation) at two weeks (David Lyon, personal communication). There is no sexual dimorphism in lengths.

WEIGHT

Neonatal 7.0 - 8.9 gms, average 8.0 gms (6 domestic, Wetherbee, 1959a); 5-6 gms (feral, Uljanin, 1941); 5 gms at 0 days, 10 gms at 4 days, 20.5 gms at 8 days, 41 gms at 16 days, 97 gms at 35 days, 120 gms at 49 days (Heinroth and Heinroth, 1928); average adult 87.6 - 90.5 gms, may reach 146 gms by fall migration (*C. c. coturnix,* Dementev and Gladkov, 1952); without sex dimorphism in weight except that females kept in captivity are much heavier than males. The quail may double its weight in autumn in conjunction with physiological *zugdisposition,* indeed the Arabic names of this bird, *Salwa* and *Summaneh* mean "to be fat" (Jones, n.d.; Wyatt, 1870).

SUBSPECIES

Coturnix coturnix africana Temminck and Schlegel 1849 is a darker, smaller race with rufous sides of head. It replaces *C. c. japonica* Temminck and Schlegel 1849 in Africa. *C. c. coturnix* (Linne 1758), larger and with black anchor band on throat and with rounded feathers on chin and throat in all plumages, replaces these races in western Asia and Europe. The nominal race was stocked unsuccessfully in North America in the nineteenth century. Recognized insular races include *C. c. conturbans* Hartert 1917 on the Azores; *confisa* Hartert 1917 on Madeira and *inopinata* Hartert 1917 on Cape Verde. The races *ussuriensis* Bogdanov 1884 of central Asia and *erlangeri* Zedlitz 1912 of Ethiopia are of doubtful validity.

FIELD IDENTIFICATION

The Common Coturnix is a cinnamon, striped galliform that runs rapidly and is smaller than the Bobwhite. Its flight is rapid, straight and low with quick wing beats and after a short distance the bird glides to the ground. Unlike the Bobwhite, they are seldom flushed in more than pairs.

The castenet-like crowing of the male, "pick-per-a-wick" with a gurgle in the middle, is distinctive. The droppings of males, with froth adhering, are sometimes diagnostic signs. The relatively broad

stripes of the spinal feathers distinguish adults from juvenals under 20 days of age. It does not perch in trees.

VOICE

A loud castanet-like crow, variably accented, "pick-per-a-wick" or "ko-turr-neex" is given by the male. This call has a brief pause between each clearly defined note and is repeated several times with a few seconds' interval between calls (Stillwell and Smith, 1880). Crowing is usually associated with the absence of a female (Moreau, 1951); it is rendered from mid-March to August (Dementev and Gladkov, 1952) and is resumed briefly in September (Jacobs, ms.), probably in association with autumnal recrudescence of the testes. The initial call occurs at five or six weeks of age. Coturnix crow during the night from 9 PM to 7 AM during the height of breeding season (Pfeifer, 1954); more pronouncedly before sunrise. In cloudy weather they crow throughout the day but are quiet during rain (Schwartz and Schwartz, 1949). In captivity they are reputed to be quiet in a lighted room but crow when the room is darkened (Montagu, 1831). The call is heard up to 200 feet (Edwards, ms.) or one-half mile (Moreau, 1951). The bird crows in an open place with neck raised, eyes shut, head on one side, and body raised at full height (Montagu, 1831); the body sinks down during the act. Historically, Japanese birds were selectively bred to trill at the end of the crow (Meise, 1954).

"Brr-up, brr-up, brr-up" ("braw-wow," close by), a subdued, hoarse, vibrating, ventriloqual call is given by both sexes (Pickford, 1945) and is said to be a mutual invitation to copulate (Naumann, 1905).

"Peu-peu" is a call given by the female, timed to coincide with the first and last syllables of the male's crow (Campbell, 1952).

Pickford (1945) records the alarm note as "pap, ata, pap-pap-pap-pap-pap." When flushed some Common Coturnix give a soft plaintive note like that of the Pectoral Sandpiper (*Erolia melanotos*) (Stillwell and Smith, 1880). The call of the very young is also disyllabic and like that of a sandpiper.

A high, cricket-like noise, "weet-weet, weet-weet" is sometimes given by the adult much like the call of the guinea fowl (*Numida pucherani*).

Ruthke (1933) records instances of calling in flight at night.

Descriptions and figures of quail-pipes used to imitate the call are given in the Encyclopaedia Britannica of 1797 (Moreau, 1951); in Rowley's Ornithological Miscellany (Newton, 1893-96); by Witherby (1903); and by Campbell (1952).

HABITAT

General.—Agricultural fields and upland grassland, especially wheat and clover, are favored. It avoids very tall and dense vegetation (Witherby *et al.*, 1941) and mountains and marshes (Jones, n.d.). Habitat is much localized and occupied variably each year.

Special.—The Common Coturnix prefers breeding areas and nesting habitat of wheat, oats, barley (Moreau, 1951), alfalfa more than six inches high (Jacobs, ms.), or clover (Westerskov, 1947). (Note: "Corn" of Old World authors is "grain," most often "wheat" in American usage, not maize). In the Canary Islands, Cullen *et al.*, (1952) found this species in open mixed forest. Migration and winter range habitat is characterized by root fields in England (Witherby *et al.* 1941), crops or short grass in Arabia (Meinertzhagen, 1954), steppes (Jones, n.d.) and heath (Cullen *et al.*, 1952).

The feeding habitat is strictly limited to the ground along peripheries of dense vegetation (Schwartz and Schwartz, 1949). In Africa, Cheesman and Sclater (1935) found them feeding in fields of dwarf millet. Roosting habitat is in the heavier marginal grass (Schwartz and Schwartz, 1949). Resting habitat is in small barren openings (Schwartz and Schwartz, *op. cit.*) where the birds often dust bathe. For refuge habitat it favors grass (Schwartz and Schwartz, *op. cit.*) or shelter under a bush or rock in flat desert (Meinertzhagen, 1954). As fields are mowed the birds leave because of the loss of standing cover (Jacobs, ms.).

DISTRIBUTION

Coturnix coturnix is found on all the Old World continents. It is migratory. Its distribution is strongly influenced by agriculture (Westerskov, 1947). In North America it has been introduced in three general stages as follows:

Stage 1.—Several thousand captured birds (*C. c. coturnix*) were imported from Sicily in 1877 - 1882, mostly under the auspices of M. G. Everts and W. Hapgood and released in the Northeast (100 as far west as Sioux City, Iowa; Tobey, 1882). These early introductions were made under the names of European, Egyptian, Messina (not "Massena Quail," *Cyrtonyx montezumae*), and Migratory Quail and were contemporaneously chronicled in *Forest and Stream.* (For bibliography see Phillips, 1928). Some of the introduced birds migrated south as far as Georgia; many reputedly returned and bred three years in succession (for bibliography see McAtee, 1944). The experiment was conceded a failure by 1885.

Stage 2.—Restaurants on the West Coast imported many thousand live *C. c. japonica* as "Migratory Chinese Quail" from 1895 to 1904; many of these escaped or were confiscated and released. Deliberate small plantings were made in the state of Washington in 1923; none survived the first year (Grinnell and Miller, 1944; Phillips, 1928).

Stage 3.—Several hundred thousand game-farm propagated Common Coturnix were stocked simultaneously as "coturnix" or "stubble" quail during the late 1950's in most of the southeastern and south-central states by the game commissions of these states in accord with a plan conceived by M. O. Steen. All or most of these birds descended from 140 breeders of the Missouri Conservation Commission and

were imported by J. W. Steinbeck of Concord, California, from Japan in 1953. Commercial propagators probably also used this same basic stock. Some of the released birds bred (an average of 62 yards from release sites in Oklahoma; Jacobs, ms.) and migrated to southern United States the year of release.

The *coturnix* race was unsuccessfully reintroduced in Ireland (Ussher and Warren, 1900); but the *japonica* race was successfully introduced in Hawaii in 1921 (Schwartz and Schwartz, 1949).

MIGRATION

The patterns of migration of this species are probably not standardized even in the Old World (Moreau, 1951). Adult males and females may migrate separately according to Alexander (1898), while Ulianin (1941) recorded that females migrate with their young. The migration flights occur at night. Moreau (1953b) gives a record of this species migrating at 57 miles per hour. Conflicting data on wind directions supposedly conducive to migration are summarized by Moreau (1953a). The Common Coturnix flies 10 to 20 feet high during migration and in compact groups of 12 to 30 birds (Meinertzhagen, 1920) or even larger (Taka-Tsukasa, 1935) although Elliott and Monk (1952) record only two or three individuals passing per minute. They separate by day (Meinertzhagen, 1954). The same author curiously records that these flights of Common Coturnix are "often accompanied by a single land rail." This is also mentioned by Pliny (Rackham, 1940) of antiquity.

Many quail perish over the sea (Gurney, 1901; Moreau, 1928), hit lighthouses (Meinertzhagen, 1924) and perch on vessels (Rackham, 1940) before arriving at their destinations. Wood (1945) records this species alighting momentarily safely on the sea. In Palestine, Meinertzhagen (1920) records the bulk of the migrants resuming their journey the evening subsequent to arrival in fall.

In the Old World a few winter in northern latitudes, i.e. England (Jones, n.d.); most arrive in Denmark in early May and leave in October; Northern Scandanavian coturnix pass through Denmark as late as the first two weeks of November (Westerakov, 1947). At Port Said, Egypt, they are found during the second week of September (Meinertzhagen, 1954). In England they arrive in March and April and leave near the end of September (Newton, 1893-96).

Interseasonal movements (*zwischenzug*) across the Mediterranean Sea of both young and old birds occur (Moreau, 1951). Migration restlessness (*zungunruhe*) is described as occurring at seven weeks of age by Heinroth and Heinroth (1928) and at six weeks by Meise (1954).

North American band recoveries show direct southerly autumnal migration of birds released in spring, summer and fall. Released birds may breed on the site or disperse several miles. Six of thirty recoveries of Common Coturnix released in Nebraska during 1957 were taken in Texas. One released in Bourbon, Kentucky, on July 9,

1957, was recovered in Saginaw, Michigan, about 107 days later (Stephens, ms.).

One bird released July 17, 1957, in Nance County, Nebraska, was recovered alive, March 11, 1958, in Hall County, Nebraska. Since six other birds of this release group were taken during the winter in Oklahoma and Texas and, since there was an absence of winter records substantiated by specimens in Nebraska, the above recovery is probably evidence of return migration.

BANDING STATUS

Banding of *C. coturnix* is administered by individual states; there is no central organization for collection of data. A representative instance is Nebraska where 23,740 were banded and released during the summer of 1957. There were 18 recoveries the following winter, all directly south in Kansas, Oklahoma and Texas. In Japan, Austin and Kuroda (1953) reported a similarly low per cent (8) recovered of 12,554 banded over twelve years. In Italy (Toschi, 1956) one per cent were recovered of one-half million banded and released on hunting areas. In France, 2.6 per cent of 2000 released were recovered within five months (Glegg, 1941).

REPRODUCTION

AGE AT MATURATION

The Common Coturnix is capable of breeding in the same year that they are hatched. Under domestication, females lay fertile eggs as early as 31 days of age and males mature sexually at 28 days (Wetherbee, 1959b). A released female that was hatched April 28 established a feral nest at 67 days of age (Edwards, ms.). The October nesting reported on Cape Verde Islands by Bourne (1955) was possibly by a bird of the year. The usual breeding is late in May and in June in England and is correlated with growth of tall grass crops (Lack, 1950).

TERRITORY

Breeding territory is advertised from a crowing ground, usually a slightly elevated spot in a clearing and bare except for a clump of vegetation. The male normally crows in the shadow of the clump. In Hawaii these crowing grounds are usually about 100 yards apart in densely populated areas, indicating the general size of territories (Schwartz and Schwartz, 1949).

PAIR-BOND

Claims of polygamy by authors (Dementev and Gladkov, 1952) are probably unsubstantiated and stem from observations of domestic birds. The Common Coturnix is probably seasonally monogamous (Coward, 1926; Moreau, 1951), except when a local surplus of females makes polygamy possible (Naumann, 1905). A description of the mating dance of the male by Pfeifer (1954) indicates that

the male jumps up and down excitedly, higher and higher to three to four feet for about one minute. It is then heard to give a nasal "wuar-wuar-wuar" while its wings are slightly elevated; the female is inattentive. The courtship is described by Bailley (1854). The male runs quickly to the female, stops along side her and keeps turning round her, dragging his wings, and stretching his neck with the feathers of his throat and breast puffed out.

Crowing by the male seems to be dependent upon the absence of the female; mated males call little (Moreau, 1951). Dementev and Gladkov (1952) indicate that the male follows the cry of the female. There is probably a mutual maintenance of the pair-bond stimulated by calling. Both male and female quail-pipes are used with success by pot hunters. In the breeding season in South Africa, Roberts (1940) noted that they often spring up in pairs, fly parallel for a time and then cross over.

COPULATION

Under domestication these birds are actively promiscuous throughout the year; females lose their spinal and cervical feathers from repeated treading by the male. The female is usually bitten on the nape during copulation. Pfeifer (1954) describes the rape of a wounded female Common Coturnix by the male. The English word, "quail" has as one of its meanings; a courtesan, in allusion to the amour of this species. When released during stocking operations, the birds often copulate on the spot before dispersing. Cross-breeding experiments (Jones, n.d.; notwithstanding) with Bobwhite *Colinus virginianus* (1500 eggs) all gave negative results (Stanford, 1957).

Male *C. coturnix* have a penis with pigmented base on the ventral cloaca. Its cloaca is usually filled with a meringue-like substance, probably secreted by a large gland on the dorsal wall of the cloaca. The histochemistry and histology of the cloacal gland and penis is described by Coil and Wetherbee (1959). The cloacal substance probably acts as an analog to secretions of the mammalian Cowper's gland, aiding in sperm transfer. The secretion adhering to the droppings cause the feet of caged birds to accumulate large balls of dung.

The testes of a sexually mature male coturnix average 15×25 mm.

NEST

The nest is well concealed in grassy cover (Schwartz and Schwartz, 1949) and looks like the nest of the Ring-necked Pheasant (*Phasianus colchicus*) but it is smaller. Outside diameter is 6 to 7 inches; inside diameter, 3½ to 4¼ inches; inside depth, 1 to 2 inches. It is constructed of dried weeds, leaves and stems placed around a shallow depression in the ground, without a canopy (Edwards, ms.). Nest building is done by the female only (Schwartz and Schwartz, 1949). Some nest are well-woven to a thickness of 1.5 cm (Uljanin, 1941) and sometimes lined with feathers (Dementev and Gladkov, 1952)

or duff but without cementing material (Edwards ms.). Most of the building is accomplished between the laying of the first and fifth eggs; none during incubation (Edwards, ms.).

EGGS

The first viable eggs are laid in early May. There is mass laying in middle May in the Chkalovskii District of U.S.S.R. and in June in the Krasnoyarsk District (Dementev and Gladkov, 1952). In Denmark forty-four per cent of the nests were found in August. Many records of eggs in September (example pictured by Westerskov, 1947) listed by Dementev and Gladkov, (1952) may be of eggs laid by birds of the year. In captivity the Common Coturnix lays throughout the year: 200 eggs per year (Cott, 1953), 250 per year (Austin and Kuroda, 1953), 365 per year (Meise, 1954).

Clutch size.—There are 6 or 7 eggs laid per clutch in Equatorial and South Africa, 6 to 8 in India, and 8 to 12 in Europe with an increase from west to east in Europe (Lack, 1947); ten is the usual number in England (Lack, 1948). In a study made in Denmark, there were 8 to 15 eggs per clutch with an average of 10.2 eggs in 17 clutches (Westerskov, 1947). In North America, Edwards (ms.) found that birds released in Ohio laid 5 to 13 eggs per clutch with an average of 8.6 eggs. He found a single replacement clutch with 7 eggs. Clutches of 17 to 20 eggs have been reported (Everts, 1878; Montagu, 1831; Dementev and Gladkov, 1952). Since individual females may lay eggs of varied shape and color, mixed clutches cannot be distinguished by these criteria. Late clutches were not found to be smaller than early ones by Westerskov (1947).

Shape.—While, in general, the eggs of this quail are of a short oval shape, they vary toward pyriform even in single clutches. Their shell texture is hard, smooth and glossy but often with a white bloom. The ground color is a light buffy yellow with chestnut to black speckles, spots and blotches, variable in extent even within single clutches. Spots can be rubbed off with the fingernail. The viteline membrane is exceedingly tough and the eggs cannot be candled by the use of simple techniques.

Size.—The average of 100 eggs from U.S.S.R. was 29.41 × 22.79 mm with maxima of 25 and 32 mm and minima of 21 and 25 mm; one clutch of 15 eggs averaged 29 × 23 mm, and had maxima of 28 and 31 mm and minima of 22 and 24 mm (Dementev and Gladkov, 1952). The average of 100 British eggs was 30.37 × 22.99 mm with maxima of 32.7 × 23.6 mm and 30.2 × 24.9 mm; and minima of 27.9 × 22.0 and 29.6 × 21.2 mm (Witherby *et al.*, 1941). In South Africa, Roberts (1940) recorded averages of 20.0 to 30.3 mm × 21.7 to 24.4 mm; in Denmark, Westerskov (1947) recorded the average of 26 eggs, 26.1 to 31.5 mm × 20.6 to 23.2 mm; and in Japan, Austin and Kuroda (1953) recorded averages of 28.8 × 22.4 mm.

The weight of fresh eggs in Germany was reported by Heinroth

and Heinroth (1928) to be 8 to 9 gms; the yolk, 3.2 gms or 35.5 per cent of the total weight. In Russia, Uljanin (1941) weighed eggs at 5.6 to 7.0 gms, two days before hatching. Eggs produced under domestication are relatively larger than those in the wild, and 10 to 15 grams is not unusual.

EGG DEPOSITION AND REPLACEMENT

The Common Coturnix lays one egg daily (Uljanin, 1941). Edwards (ms.), in field-pen studies, found no dump nests as in pheasants. The same investigator found that a clutch of 9 eggs that had been incubated 10 days was replaced 10 days after being disrupted; and a clutch of 6 eggs that had been incubated 6 days was replaced by 7 incubated eggs 11 days after the date of disruption. A clutch of 26 eggs was thought by Witherby *et al.* (1941) to be laid by two females. Laying birds deposit larger fecal droppings.

Incubation attentiveness.—Incubation begins on completion of the clutch (Witherby *et al.*, 1941) and is performed by the female only. She has an incubation patch (Austin and Kuroda, 1953; Edwards, ms.; Dementev and Gladkov, 1952). The latter authors record the unusual occurrence of two different males (sex determined by dissection) incubating in Russia and with well-developed incubation patches. The female does not flush easily (Whitehead, 1909) and is often killed on the nest. Edwards (ms.) found that the sitting bird can be lifted off the eggs with subsequent desertion; however, it does desert if the nest or eggs are damaged. The hen was not known to share incubation with others in Edwards' study. Large clutches of eggs were said to be layered during incubation (Stillwell and Smith, 1880).

Incubation period.—The average minimum time required for

Fig. 1.—Sternum, corocoid, furculum and ventral ribs of just-hatched *Coturnix coturnix* (left) and *Lophortyx californicus* (right) compared. Although the former hatches in only sixteen days and latter in twenty-three days, the bones of the former are much further ossified at hatching. A striking feature of the life history of *C. coturnix* is its accelerated ontogeny.

hatching of 100 commercial eggs was 395 hours (16.4 days) with a range from 380 to 432 hours under artificial incubation of 99.5°F. dry bulb, 89°F. wet bulb, forced draft (Wetherbee, 1959b). Heinroth and Heinroth reported incubation periods of 16 and 17 days (1928). The body temperature of 110°F. of the Bobwhite (*Colinus virginianus*) was found to be the same for *Coturnix coturnix* by Jacobs (ms.) in spite of 7 days' difference between these two species in incubation period. Furthermore, Wetherbee (1959) found that newly-hatched *C. coturnix* exceed Bobwhite and other quails in extent of ossification in spite of the difference of a week in incubation periods. (See Figure 1.) Line drawings of embryos for each of the 16 days of incubation were made by Edwards (ms.). There is a two-day interval between the hatching of the first and last chick of the brood according to Dementev and Gladkov (1952) and Jacobs (ms.). The brooding hen readily adopts fostered offspring (Jones, n.d.).

Flightless period.—The young leave the nest a few hours after hatching and are brooded by the female only (Heinroth and Heinroth, 1928). They disperse as far as 100 meters four days after hatching (Dementev and Gladkov, 1952). Broods average five young in Hawaii (Schwartz and Schwarts, 1949). Weight of newly hatched young is about 8 grams. The temperature-regulatory mechanism is not fully developed at hatching; homiothermy was not found in the tested range of 28 to 37°C. by Boni (1942). The young fly short distances at 11 days of age and fly strongly at 19 days (Heinroth and Heinroth, 1928).

Number of broods per year.—There are conflicting evidences regarding the number of broods produced per year. Uljanin (1941) is dogmatic in stating that this species is single-brooded in all latitudes of U.S.S.R. Records of multiple broods are attributed to replacement clutches, to variability of reproductive readiness of the female (Dementev and Gladkov, 1952) and to birds of the year perhaps breeding in the fall since they mature sexually under domestication in 4 weeks. The Common Coturnix is reputed by Berthet (1949) to reproduce in Africa during the winter and again the same year in Europe after migration.

SURVIVAL

Rate of survival.—In Japan, 1007 recoveries from 12,554 banded Common Coturnix in the period 1925 to 1937 show a shooting toll of only 8 per cent, which is low for a game species. As 89.4 per cent of the recoveries were taken within the first year after banding, 9.3 per cent, the second year, and only 1.2 per cent survived into the third year, an average annual mortality of about 90 per cent is indicated and it follows that there is a population turnover of practical completeness every two years (Austin and Kuroda, 1953). The potential life span of individuals would be expected to be brief considering the acceleration of other aspects of the birds' development.

There are great fluctuations in population levels and the species may well be "cyclic" on the Cape Verde Islands (Bourne, 1955). Westerskov (1947) correlated cyclic high populations with invasions by Asiatic Pallas's grouse (*Syrrhaptes paradouxus*) in Denmark. "Quail years" are listed by Saunders (1947) in England and by Westerakov (1947) in Scandinavia. The species has apparently decreased markedly in numbers in the last half century in Japan (Austin and Kuroda, 1953). In England it is just recovering after a long period of virtual extirpation (Moreau, personal communication).

Decimating agents.—Foxes, ermine, skunks, hamsters and hawks are listed as enemies of this quail by Dementev and Gladkov (1952); the crow (*Corvus brachyrhynchos*), Swainson's Hawk (*Buteo swainsoni*), snakes and harvest machines are mentioned by Jacobs (ms.). Owls expectedly take a heavy toll considering the nocturnal activity of the coturnix (Blanchet, 1939). Strung wires and other human agencies, especially for sport and market, are important decimating agents. Migration hazards seem to be of great importance. During migration lighthouses kill many quail (Meinertzhagen, 1924; Westerskov, 1947; Ticehurst, 1924). After a short spell of sea-fog, ships off the coast of Egypt sailed for an hour through floating masses of drowned quail (Moreau, 1928); Gurney (1901) found 8 to 10 Common Coturnix in the stomachs of sharks off the coast of France. In autumn practically the entire length of the north coast of Egypt is lined with nets and snares (Moreau, 1928). Post-harvest operations, i.e. the baling of windrows, may be more dangerous than the actual reaping of crops (Campbell, 1952).

Diseases and parasites.—The Common Coturnix is highly resistent to ulcerative enteritis (of uncertain infective agency) of Bobwhite (Kirkpatrick and Moses, ms.). Dr. F. R. Woodring (personal communication) found the Common Coturnix to be susceptable to erysipelas of turkey and swine in Nebraska. This disease is bacterial (*Erysipelothrix rhusiopathiae*) and communicable to man. The coccidium *Eimeria coturniceps* was found in the Common Coturnix in India (Chakravarty and Kar, 1946). The cestodes *Raillietina vivieni* in Indochina (Joyeux and Baer, 1935) and *Melroliasthes lucida* in England (Clapham, 1935) have been recorded. Likewise the following nematodes are listed as parasitizing coturnix: *Subulura coturnicis* (Yamaguti, 1941) in Japan and *Allodapa skrijabini* Semjonoff 1926, *A. noctuae gallinae* Semjonoff 1926, *A. suctoria* (Molin 1860), *Acuaria coturnicola* Semjonoff 1926, *Heterakis vesicularis* (Frohlich 1791), *Ascaridia compar* Schrank 1791 (or 1790?), *Harlertia obesa* Seurat 1915, *Cyrnea eurycerca* Seurat 1914 and *Agamospirura* sp. in the Don Region of U.S.S.R.; 39 per cent of 110 *C. coturnix* examined had these nematodes. Males were most frequently parasitized. The worms were most abundant in the small intestine but were also found in the caecum, under the corneus of the gizzard and in the bursa of Fabricius (Semjonoff, 1926). Cram

(1927) reported *Heterakis gallinae* Gmelin 1790. Ptushenko in the U.S.S.R. noted many tape worms in the young especially during drought (Demenkov and Gladkov, 1952). In Hawaii, Schwartz and Schwartz (1949) listed a hippoboscid fly, mites on head and primaries, lice and eye-worms.

Food

The Common Coturnix consumes a proportionately higher ratio of animal matter to vegetable matter than does the Bobwhite (Schwartz and Schwartz, ms.). These authors found that 21 stomachs in Hawaii contained 42 per cent animal matter and 58 per cent seeds by volume. The animal matter consisted mostly of insects and snails of the grass or ground-dwelling species, not of the flying or quickly moving insects. Kerc *et al.* (n.d.) lists 28 species of Coleoptera and 17 other forms of insects and 7 species of gastropods. Schwartz and Schwartz (1949) list 27 economically injurious animal forms from stomachs of Common Coturnix in Hawaii. Dementev and Gladkov (1952) list "snout beetles," Formicidae, Tineidae, Muscidae and other Arthropoda. In years of locust abundance this bird eats locusts in great quantities — but also the preying mantes. In Morocco, Meinertzhagen (1940) found this quail eating the small water snail, *Cochlicella acuta obesa* in fall. Witherby *et al.* (1941) note especially the larvae of *Agrotis*.

Seeds, mostly fallen seeds, (Stillwell and Smith, 1880; Dementev and Gladkov, 1952) are the chief vegetable matter eaten. Rice, wheat (Jones, n.d.), sesame (Bucknill, 1910), plantain and chickweed (Saunders, 1927), *Lolium, Brassica, Polygonom, Chenopodium, Rumex, Spergula, Stellaria, Plantago, Papayer, Vicia* (Witherby *et al.*, 1941) and *Ballota* (Dementev and Gladkov, 1952) seeds predominate. Kerc *et al.* (n.d.) list seeds of more than 130 forms from 28 families of plants in Hungary; Schwartz and Schwartz (1949) list seeds of more than 46 kinds for Hawaii. Berries of *Daphne gnidum* are a staple on the Canary Islands (Cullen *et al.*, 1952). Common Coturnix are not made sick by feeding upon *Aethusa cynapium* (poison hemlock) but may thereby become poisonous to a person who eats the flesh of the birds (Heim, 1928); this fact was experimently confirmed by Sergent (1941). Green matter is only rarely taken in the wild (Jones, n.d.; Kerc *et al.*, n.d.; Meinertzhagen, 1940) but is readily taken in captivity in the absence of water (Schwartz and Schwartz, 1949). Dementev and Gladkov (1952) mention sprouting plants as food. Their water requirements are apparently fulfilled by the insect diet (Schwartz and Schwartz, 1949) and by dew (Jones, n.d.) but they drink great quantities of water in captivity. In dry climes (Bourne, 1955) and in drought (Dementev and Gladkov, 1952) they drink from rivers and oases.

Grit is taken into their crops and stomachs (Schwartz and Schwartz, 1949; Dementev and Gladkov, 1952; Jones, n.d.).

HABITS

C. coturnix is most active at night and twilight (Dementev and Gladkov, 1952; and many other authors) and it is more susceptible to heat prostration than is the Bobwhite (Jacobs, ms.). Most of its food is taken in late afternoon; most birds collected in the morning or early afternoon had empty crops (Schwartz and Schwartz, 1949). Jones (n. d.) and others report dust bathing at noon.

Socially, the male is pugnacious toward competitors and toward its mate, while the female is less aggressive. Before egg laying in June, when flushed, the pair keep in close proximity (Ingram, 1908). While not otherwise gregarious, family bevies of both sexes unite to dust bathe but there is no permanent bevy formation (Schwartz and Schwartz, 1949). Migrating flocks, which may be large (Taka-Tsukasa, 1935), separate by day (Meinertzhagen, 1954). The male is so persistent at copulating in captivity that the female is unable to incubate; therefore, it is thought by game-breeders that the female must hide from him in the wild. Undoubtedly under natural conditions there is less aggression. Wild Common Coturnix often frequent poultry yards with domestic chickens in the Old World. They are difficult to flush except by dogs (Coward, 1926). They seldom rise twice (Meinertzhagen, 1954) and are often stepped upon. Sometimes when flushed by one sportsman, the birds fly blindly toward another (Gurney, 1901). The flight is swift, with rapid wing beats, direct, very low (6 - 15 ft.) and of flat and short trajectory (about 50 yards), ending with an indifferent glide; the bird usually remains where it alights (Schwartz and Schwartz, 1949). Even when several birds are found together they generally rise singly or in pairs (Jones, n.d.). Occasionally while in the air their flight changes to a "beautiful hovering motion" (Jones, n.d.). On the ground the bird runs swiftly to hide from danger (Dementev and Gladkov, 1952) — this may be in contradiction to Schwartz and Schwartz, above. It runs quickly and lightly but ungracefully with its very small tail hanging down and its neck drawn in, each step being accompanied by a slight nod of the head (Jones, n.d.). The English verb "to quail" takes its meaning from the habit of this bird of cowering from danger. It does not perch and at night (or day, as the case may be) roosts separately, even during very cold weather (Stanford, 1957).

ADAPTABILITY

It is ironic that this, the first bird species domesticated by man (The Mastaba of Mereruka, pt. 2, University of Chicago Art Institute, Sakkarah Expedition, 1938) should only in the 20th century be recognized for its potentialities as a pilot species for biological laboratory research. The adaptability of the bird to battery breeding cages, its prolificacy, and its accelerated ontogeny make it analogous to the white rat or fruit fly in its utility for laboratory experiments.

REFERENCES

AUSTIN OLIVER L., JR. AND NAGAHISA KURODA 1953. The birds of Japan, their status and distribution. *Bull. Mus. Comp. Zool.*, **109**:175-637.

BAILLY, J. B. 1854. Ornithologie de la Savoie. Bailly, Paris. 201 p.

BERTHET, G. 1949. La nidification tardive des Cailles et l'hypothese de le double nidification de cette espece sur les deux continents. *Nos Oiseaux*, **20**:34-35.

BLANCHET, MAURICE 1939. Notes de route de la region des Causses. *Arch. Suisses Ornithol.*, **1**:451-454.

BONI, A. 1942. Ueber die Entwicklung der Temperature Regulation bei verschiedenen Nesthockern. *Arch. Suisses Ornithol.*, **2**:1-56.

BOURNE, W. R. P. 1955. The birds of the Cape Verde Islands. *Ibis*, **1955**: 508-556.

BUCKNILL, JOHN A. 1910. On the ornithology of Cyprus. *Ibis*, **1910**:385-435.

CAMPBELL, W. D. 1952. Some observations on quail during the breeding season of 1951. *British Birds*, **45**:167-170.

CHAKRAVARTY, M. AND A. B. KAR 1946. A study of the coccidia of Indian Birds. *Proc. Roy. Soc. Edinburgh*, **62B**:225-233.

CHEESMAN, R. E. AND W. D. SCLATER 1935. On a collection of birds from northwestern Abyssinia. *Ibis*, **1935**:151-191.

CLAPHAM, P. A. 1935. Some helminth parasites from partridge and other English birds. *J. Helminth.*, **13**:139-148.

CLARK, HUBERT LYMAN 1918. Tail-feathers and their major upper coverts. *Auk*, **35**:113-123.

COIL, WILLIAM H. AND DAVID K. WETHERBEE 1959. Observations on the cloacal gland of the Evrasian quail, *Coturnix coturnix*. *Ohio J. Sci.*, **59**:268-270.

COTT, HUGH B. 1953. Egg exploitation of wild birds. *Ibis*, ***1953***; 409-449: 643-675.

COUES, ELLIOTT, 1903. Key to North American birds, Vol. 2. The Page Co., Boston. 616 p.

COWARD, T. A. 1926. The birds of the British Isles and their eggs. Frederick Warne and Co., Ltd., London. 376 p.

CRAM, ELOISE 1927. Bird parasites of the nematode suborders Strongylata, Ascaridata, and Spirurata. *U. S. Nat. Mus. Bull.*, **140**:465.

CULLEN, J. M., P. E. GUITON, G. A. HORRIDGE AND J. PEIRSON 1952. Birds on Palma and Gomera (Canary Islands). *Ibis*, **1952**:68-84.

DEMENTEV, G. P. AND H. A. GLADKOV 1952. Birds of the Soviet Union. Vol. 4, p. 133-148. (In Russian.)

EDWARDS, WILLIAM R. Unpublished manuscript. Completion Report, P. R. Proj., Ohio. W-103-R. 1957.

——— Unpublished manuscript. A guide to ageing coturnix embryos, P. R. Proj., Ohio. 1957.

ELLIOTT, H. F. I. AND J. F. MONK 1952. Land-bird migration over the Suez route to east Africa. *Ibis*, **1952**:528-530.

EVERTS, MARTIN G. 1878. Successful breeding of the Messina quail. *Forest and Stream*, **11**:56.

GLEGG, W. E. 1941. The birds of "l'Ile de la Camargue et la Petite Camargue." *Ibis*, **1941**:556-610.

GRINNELL, JOSEPH AND ALDEN H. MILLER 1944. The distribution of the birds of California. *Pacific Coast Avifauna*, **27**:1-608.

GURNEY, J. H. 1901. On the ornithology of the Var and the adjacent districts. *Ibis*, **1901**:362-407.

HEIM, DE BALSAC H. 1928. Sur le regime alimentaire de la caille. *Rev. Franc. Ornithol.*, **1928**:396-397.

HACHISUKA, M. 1931. On the eggs of the Japanese quail. *Bull. British Ornith. Club*, **52**:37-38.

HEINROTH, OSKAR AND MAGDALENA HEINROTH 1928. Die Vogel Mitteleuropas. Vol. 3. Hugo Bermuhler, Berlin. 286 p.

INGRAM, COLLINGWOOD 1908. Ornithological notes from Japan. *Ibis*, **1908**: 129-169.

JACOBS, KARL. Unpublished manuscript. Completion Report, P. R. Proj., Oklahoma, W-65-R-2. 1957.

JONES, THOMAS RYDER. No date. Cassell's Book of Birds from the text of Dr. Brehm, Vol. 3. Cassell, Peter and Galpin, London. 312 p.

JOYEUX, CH. AND J. G. BAER 1935. Cestodes d'Indochine. *Rev. Suisse Zool.*, **42**:249-273.

KERC, A., Z ZSAK AND Z. KASZAB. No date. The agricultural significance of the quail. *Magyar Nemzeti Museum; Annales Historico Naturales*, **4**:197-209.

KIRPATRICK, C. M. AND HAROLD E. MOSES 1957. Resistance of Japanese quail to ulcerative enteritis (UE) of bobwhites. Unpublished manuscript.

KURODA, NAGAMICHI 1924. A note on the Japanese quail. *Auk*, **41**:116-123.

LACK, DAVID 1947. The significance of clutch-size. *Ibis*, **1947**:302-352.

——— 1948. The significance of clutch-size. *Ibis*, **1948**:25-45.

——— 1950. The breeding seasons of European birds. *Ibis*, **1950**:288-316.

LYON, DAVID. Personal Communication. Growth, weight, and plumage development of Coturnix quail, 1957.

MCATEE, W. L. 1944. The European migratory quail in North America. *Auk*, **61**:652.

MEINERTZHAGEN, R. 1920. Notes on the birds of Southern Palestine. *Ibis*, **1920**:195-259.

——— 1924. Birds at Egyptian lighthouses. *Ibis*, **1924**:643-644.

——— 1954. Birds of Arabia. Oliver and Boyd, London. 624 p.

MEISE, WILHELM 1954. Uber Zucht, Eintritt der Geschlectsreife, Zwischenund Weiterzug der Wachtel (*C. coturnix*). *Vogelwarte*, **17**: 211-215.

MONTAGUE G. 1831. Ornithological dictionary of British birds. Ed. 2. Hurst, Chance and Co., London. 592 p.

MOREAU, R. E. 1928. Quail. *Bull. Zool. Soc. Egypt*, **1**:6-13.

——— 1951. The British status of the quail and some problems of its biology. *British Birds*, **44**:257-276.

——— 1953a. Migration in the Mediterranean area. *Ibis*, **1953**:329-364.

——— 1953b. Migrants on the north coast of Spain. *Ibis*, **1953**:375-376.

NEWTON, ALFRED 1893-1896. A dictionary of birds. Adam and Charles Black, London. 1088 p.

NAUMANN, J. F. 1905. Naturgeschichte der Vogel Mitteleuropas. Vol. 6. Gera-Untermhaus, Leipzig. 337 p.

PHILLIPS, JOHN C. 1928. Wild birds introduced or transplanted in North America. *U. S. Dept. Agriculture Tech. Bull.* 61. 63 p.

PICKFORD, K. D. 1945. Observations on quail in Glouchestershire and their calls, *British Birds*, **38**:257-259.

PFEIFER, SEBASTIAN 1954. Vergewaltingung eines verletzen Wachtelweibchens durch ein Wachtelmannchen (*Coturnix coturnix*). *Ornithologische Mitteilungen*, **6**:174-175.

RACKHAM, H. 1940. Pliny's Natural History, 10. Wm. Heinemann, Ltd., London., p. 33.

ROBERTS, AUSTIN 1940. The birds of South Africa. H. F. and G. Witherby, Ltd., London. 463 p.

RUTHKE, PAUL 1933. Vermischte Mitteilungen. *Beitr. Fortpflanzungbiol. Vogel*, **9**:186-193.

SAUNDERS, HOWARD 1927. Manual of British birds. Gurney and Jackson, London. 834 p.

SCHWARTZ, CHARLES W. AND ELIZABETH REEDER SCHWARTZ 1949. A reconnaissance of the game birds in Hawaii. Hawaii Board of Commissioners of Agriculture and Forestry, Hilo, Hawaii. 168 p.

——— Unpublished manuscript. A comparison of the foods of *Coturnix* with three other gallinaceous birds. Missouri Conservation Commission.

SEMJONOFF, W. D. 1926. The nematode fauna of the quail. *Wissenschaftliche Mitteilungen Universitat Smolensk*, **3**:87-07. (In Russian)

SERGENT, E. 1941. Les cailles empoisonneuses dans la Bible — et en Algerie des nos jours. Apercu historique et recherches experimentales. *Archives de l'Institute Pasteur D'Algerie*, **19**:161-192.

SHIMAKURA, K. 1940. Notes on the genetics of the Japanese quail. 1. The simple Mendelian, automsomal, recessive character, "brown-splashed white" of its plumage. *Japanese J. Genetics*, **16**:106-112. (English summary).

STANFORD, JACK A. 1957. A progress report of coturnix quail investigations in Missouri. *Trans. North American Wildlife Conf.*, **22**:316-357.

STEJNEGER, LEONHARD 1885. On the shedding of the claws in the ptarmigan and allied birds. *Ibis*, **1885**:50-52.

STEPHENS, CHESTER H. Unpublished manuscript. Quarterly Progress Report, P. R. Proj., Kentucky. 1957.

STILLWELL, E. M. AND EVERETT SMITH 1880. Report of the Commissioners of Fisheries and Game, of the State of Maine for 1880. 24 p.

STURNIOLO, G. 1913. Un caso di melanismo completo nella *Coturnix communis* (Bonn). *Riv. Italiana Ornithologica*, **2**:202-203.

TAKA-TSUKASA 1935. The birds of Nippon. Vol. 1. Witherby, London, p. 204-238.

TICEHURST, CLAUDE B. 1924. Birds for the Red Sea lights. *Ibis*, **1924**:282-283.

TOBEY, HORACE P. 1882. Letter. *Forest and Stream*, **18**:28.

TOSCHI, AUGUSTO 1956. Experienze sul somportamento de quaglie (*Coturnix c. coturnix*) (L) a migrazione interrotta. *Richerche de Zoologia applicata alla Caccia*, **27**:1-275.

ULJANIN, N. 1941. Materials on ecology of the quail in north Kasahstan. *Arch. Mus. Zool., Moscow*, **6**:153-166. (In Russian)

USSHER, RICHARD J. AND ROBERT WARREN 1900. The birds of Ireland. Gurney and Jackson, London. 419 p.

WESTERSKOV, KAJ. 1947. Vagtlens (*Coturnix c. coturnix* (L.) Udbredelse og Lavevis i Danmark. *Dansk Ornithologisk Forenings Tidsskrift*, **41**:89-111.

WETHERBEE, DAVID KENNETH 1959a. Comparative phylembryogenetic dimensionality of neonatal birds. University Microfilms, 260 pp. Ann Arbor, Michigan.

——— 1959b. Artificial incubation of wild birds' eggs and developmental condition of neonates. University Microfilms, 59:3872:1-153. Ann Arbor, Michigan.

WHITEHEAD, C. H. T. 1909. On the birds of Kohat and Kurram, northern India, 2. *Ibis*, **1909**:214-284.

WINT, GEORGE 1957. One in seventy thousand. *Oklahoma Wildlife*, (October, 1957):11.

WITHERBY, HENRY F. 1903. An ornithological journey in Fars, south-west Persia. *Ibis*, **1903**:501-571.

——— F. C. R. JOURDAIN, NORMAN F. TICEHURST, BERNARD W. TUCKER 1941. The handbook of British birds. Vol. 5. Witherby, London. p. 250-254.

WOOD, K. A. 1945. Quail alighting on the sea. *British Birds*, **38**: 198.

WYATT, CLAUDE W. 1870. Notes on the birds of the Peninsula of Sinai. *Ibis*, **1870**:1-18.

YAMAGUTI, SATYU. 1941. Studies on the helminth fauna of Japan. *Japanese J. Zool.*, **9**:441-480.

Grit as an Ecological Factor[1]

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ABSTRACT: The pheasant, a highly granivorous species, succeeds best in areas of high calcium concentration. Grains are normally low in calcium content, hence lime-containing grits act as a necessary source of this element. Gravel of the proper chemical composition is particularly significant in the diet of growing birds, and probably for hens during the laying season.

Recently glaciated regions where the till possesses high calcium characteristics represent the most suitable pheasant ranges. An example of this is the Minnesota, Dakota and northern Iowa area.

The indications are that grit possessing large amounts of magnesium, even though adequate in calcium, is undesirable and may even be deleterious.

The first to suggest a possible ecological role for grit was Leopold (1931). In discussing the peculiar distribution of pheasants and Hungarian partridge in the upper midwest, he hypothesized that various dietary factors, which included grit, might be responsible.

Data herein reported cover studies relating to the importance of grit in the welfare and distribution of the ringneck pheasant (*Phasianus colchicus*). Three aspects of the problem are recognized: 1) evidence for any nutritional relationship specific enough to be ecologically significant; 2) problems relative to measuring grit adequacy; and 3) evidence, positive or negative, that grit is important in pheasant ecology under natural conditions.

For gallinaceous birds, gravel (as a grinding agent) is generally recognized as an aid to the gizzard. However, any material hard enough to act as an abrasive seems to suffice; therefore, in this role the need for grit seems hardly singular enough to have ecological importance.

McCann (1939) has demonstrated that grit is also a source of required nutrient for the pheasant and must be classified under the category of a critical food. By using young, growing pheasants and feeding measured quantities of insoluble gravel (quartz) it was demonstrated that grit consumption quickly rose to extravagant levels with a manifest, frenzied craving for grit, which prevailed over their appetite for normal organic food. This reflected a nutritional need, since feeding with a supplement of bone meal (primarily tri-calcium phosphate) resulted in an almost immediate return to normal grit consumption. In another similar experiment, gravel consisting of glacial

[1] Funds for this study were supplied by the National Science Foundation. Facilities were graciously provided by the College of St. Thomas, St. Paul, Minn., and consulting advice was given by the Department of Chemistry, College of St. Thomas. Population data was made available by the Bureau of Game Research, Minnesota Division of Game and Fish.

till (low in phosphorous) had the same satisfying effect; and in still another experiment, powdered calcium carbonate produced a similar decline in grit consumption. These experiments indicated, therefore, that for the growing pheasant, grit is essential as a dietary source of the mineral element calcium.

According to the experiments of Dale (1955) with pheasants, calcium can also be critically important in the physiology of reproduction. And in this regard, recent studies reported by Hammond (1954) reveal that poultry, close relatives to the pheasant, store only enough calcium for six eggs, and that calcium is stored for no longer than ten days prior to egg laying.

Further evidence of the specific nutritional qualifications of gravel was indicated in an experiment by McCann (1938; 1939) in which experimental pheasants refused to utilize dolomitic limestone as a source of grit. This was interpreted as a deliberate abstention, since in every other study the birds consumed at least small daily quantities of any other type of grit.

More clearly suggestive of the inadequacy of grit with high magnesium content is the evidence with poultry. Alder (1927) found that pullets, after being fed dolomite grit for four months, became ". . . extremely nervous, very sensitive, and easily frightened. Production decreased, and the shell of the eggs became progressively thinner. Practically every bird in the pen developed diarrhœa or became very loose, as indicated by the droppings and badly soiled condition of the feathers of the abdomen. All of these conditions cleared up in a short time after substituting a practically pure carbonate limestone. . . ." He concludes that since magnesium forms a part of most deposits

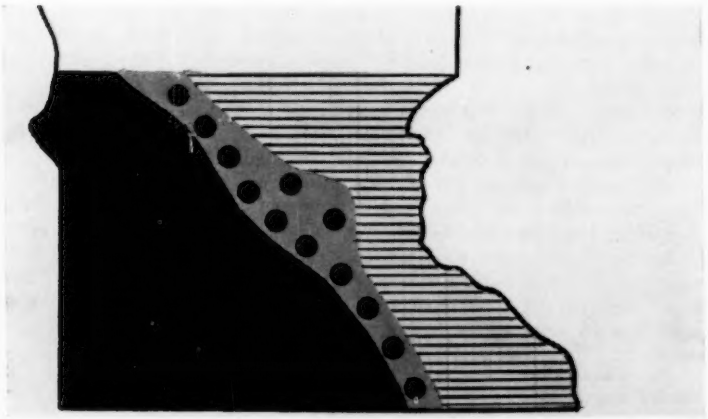

Fig. 1.—Relative abundance of pheasants in the state of Minnesota. (Solid: excellent to good; dotted: good to fair. Horizontal lines: fair to poor.)

resulted in growing chicks from adding 0.5 per cent magnesium to their diet, offered as carbonate. Buckner, Martin, and Inkso (1932) of limestone, limestone should not be used unless found free of magnesium. Mussehl, et al. (1930) found that a tendency toward rickets found that the addition of magnesium carbonate to the diets of chicks disturbed the calcium and phosphorous balance necessary for the normal formation of bones during the first six weeks' growth.

Significant to determining the chemical adequacy of grit is the fact that minerals are absorbed from food under the action of hydrochloric acid having a pH of 2.0 (Farner, 1942; Jull, 1951). Accordingly, the following technique of grit analysis was developed: to 15 grams of gravel is added 200 ml of .010N hydrochloric acid. This is then placed on a mechanical shaker for 15 minutes to simulate the action of the gizzard. Following this, a 50 ml aliquot is titrated, using the Versene method of calcium analysis with calcein as the indicator. The results are expressed as milligrams of $CaCl_2$ per 50 ml.

This technique proves particularly effective for low calcium samples, but it does not assay fully the calcium availability of high calcium samples, since 200 ml of acid is neutralized in less than 15 minutes under the influence of large quantities of calcium carbonate. Nevertheless, for practical purposes, the method reveals significant differences in calcium availability.

In the state of Minnesota, pheasants are most abundant in a triangular area covering the western and southern portions of the state (Fig. 1). To the east of this region, pheasant numbers gradually decline.

Pheasant population data was obtained from the Minnesota Division of Fish and Game. The information represents the accrued data from annual roadside censuses conducted since the 1940's. Numbers are expressed as birds per mile, on a county basis. Concurrently, sifted grit samples were collected from preselected collection sites. The collected samples were then analyzed chemically, using the method described.

The results, including population figures and grit analysis, are superimposed on the map of Minnesota in Figure 2. The data appear in the form of fractions, the upper figure representing the grit analysis results; the lower figures representing the population level for the county in question.

In the area of high pheasant abundance, to the west of the thin, oblique line (Fig. 2), the grit samples test homogeneously high in calcium content. In contrast, to the east both pheasant numbers and grit calcium figures are conspicuously low. For reasons previously described, the available calcium in the high-testing samples is no doubt even more surpassing.

The glacial till in the two areas is known to have had different origins. The western and southern areas of the state were glaciated by ice from the Keewatin Ice Center west of Hudson Bay, and the eastern areas of the state were covered by ice from the Labrador Ice

Center in northeastern Canada. Along the points where the two types of till meet, there appears to be considerable intermixing.

The southeastern corner of the state is unusual in never having been glaciated. The soil here consists of fine, wind-deposited loess, layed down during interglacial times. Grit in this soil is physically lacking. Outcroppings of ancient limestone occur in this area, but according to Prokopovitch and Schwartz (1956) much of this is dolomitic, in which the magnesium content is as high as 42 per cent. Crushed rock of this same material, in the absence of conglomerate gravel, is used as a road surfacing. Pheasant numbers in the counties of this area are notably low, averaging only 0.68 birds per mile for the entire area.

Two random grit samples were collected from western Wisconsin, which according to Dale (1955) is conspicuous for its low pheasant population. A random sample from St. Croix County contained 1.43 mgs of calcium; a similar sample from Pierce County tested 0.39 mgs. In contrast, two random grit samples from South Dakota, a state which is outstanding for its normally high pheasant numbers, tested as follows: a random sample from Codington County, 16.38 mgs; a random sample from Miner County, 18.59 mgs.

From the foregoing evidence it is the contention of the writer that grit of the proper chemical makeup (i.e., high calcium; low magnesium) is an ecological factor of paramount importance for the pheasant. In many situations it transcends in significance the factors of climate, cover, or any particular organic food. This is in harmony with the statement of Dale (1955) that the pheasant in North Amer-

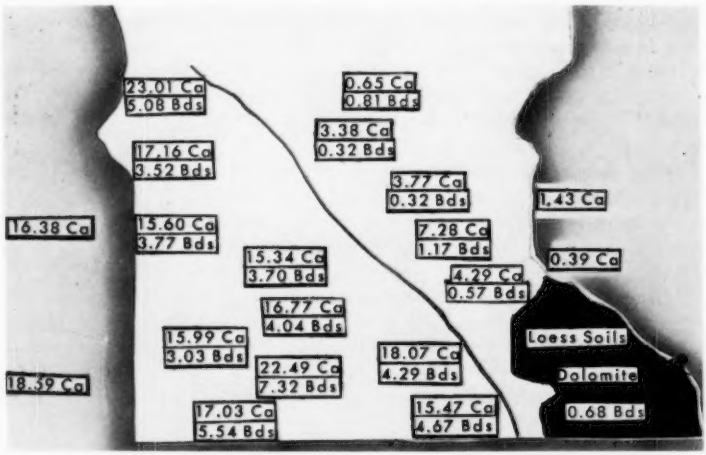

Fig. 2.—Grit-contained calcium, expressed in milligrams, compared with pheasant numbers, expressed as birds per mile. Figures from Wisconsin and South Dakota show only the calcium levels.

ica seems to have had its greatest success in areas with calcareous soils. It is the chemical nature of the grit, however, that evidence indicates is determinant.

Discussion

The reason calcium-containing grit is so vital in the diet of pheasants probably arises from the fact that cereal grains play such an important part in their diet. Grains are known to be deficient in the mineral element calcium. This being the case, one might anticipate that the Hungarian partridge (*Perdix perdix*) would be as acutely influenced by the chemical nature of grit as is the pheasant, since the two species are about equally granivorous.

One might also speculate that among many other species of birds the need for calcium-containing grit is much less stringent and therefore less important ecologically. The grouse (*Bonasa umbellus*) has a diet comprising large quantities of herbaceous material and is equipped with large colic caeca which aid in extracting nutrient of low concentration. Its diet and digestive anatomy are somewhat comparable to those of a rabbit, and thus the grouse probably has no vital need for calcareous grit.

The raptorial species, which utilize the entire bodies of small vertebrates, more than likely have all their calcium requirements supplied by the endoskeletons of their natural prey.

Species whose diets are made up of large amounts of certain invertebrate animals may also be supplied with adequate amounts of mineral in their organic diet. Earthworms with their caliciferous glands and terrestrial mollusks with their calcareous shells might be rich sources, to cite two examples.

Work by Grimshaw, *et al.* (1958) which shows a high level of calcium in caterpillar frass suggests the ability of insect larvae to concentrate this element, and thus to serve as a possible dietary source of calcium.

References

Alder, Byron. 1927. The use of calcite and other natural deposits of calcium carbonate in the ration of laying hens. *World's Poultry Congress Report.* pp. 231-234.

Buckner, G. D., J. H. Martin, and W. M. Inkso, Jr. 1932. The effect of magnesium carbonate when added to diets of growing chicks. *Poultry Sci.*, **2**:58-62.

Dale, Fred H. 1955. The role of calcium in reproduction of the ring-necked pheasant. *J. Wildlife Management*, **19**:325-331.

Farner, Donald S. 1942. The hydrogen ion concentration in avian digestive tracts. *Poultry Sci.*, **21**:445-450.

Grimshaw, H. M., J. D. Ovington, M. M. Betts and J. A. Gibb. 1958. The mineral content of birds and insects in plantations of *Pinus Sylvestris* L. *Oikos*, **9**:26-34.

Jull, Morley A. 1951. Poultry husbandry. McGraw-Hill Co., New York. 526 p.

Hammond, John (Editor). 1954. Progress in the physiology of farm animals. *Butterworth Scientific Publications*, London. Vol. 1. 392 p.

LEOPOLD, ALDO. 1931. Report on a game survey of the north central states. *Sporting Arms and Ammunition Mfg. Institute*, Madison, Wisconsin. 299 p.

MCCANN, LESTER J. 1938. Master's Degree Thesis. Entomology and Economic Zoology Department, Univ. of Minn., St. Paul, Minn. 49 p.

———. 1939. A study of the grit requirements of certain gallinaceous game birds. *J. Wildlife Management*, **3**:31-41.

MUSSEHL, F. S., R. S. HILL, M. J. BLISH AND C. W. ACKERSON. 1930. Utilization of calcium by the growing chick. *J. Agr. Res.* **40**:191-199.

PROKOPOVICH, NIKOLA, AND GEO. M. SCHWARTZ. 1956. Minnesota limestone suitable for Portland cement. Minn. Geol. Sur., Univ. of Minn., Minneapolis, Minn. Summary Report No. **8**:1-39.

Observations on the Life Histories of Turtles (Genus Pseudemys and Graptemys) in Lake Texoma, Oklahoma

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ABSTRACT: Aspects of the life histories of *Pseudemys scripta elegans* and *Graptemys pseudogeographica ouachitensis* (Reptilia: Testudines) were studied in Lake Texoma, Oklahoma. Variation in the color patterns of the two species is considered. Males of *Pseudemys* are sexually mature at a plastron length of 9.0 to 10.0 cm; females at 17.4 to 19.3. The realized annual reproductive capacity of a female *Pseudemys* is estimated to be 26.4 eggs (3 clutches; 8.8 eggs per clutch). Some males become sexually mature in their third year; females in their fourth. Males of *Graptemys* are sexually mature at a plastron length of 7.0 cm; females at 15.0 cm. Each *Graptemys* female lays approximately 19.5 eggs per year (3 clutches; 6.5 eggs per clutch).

The elongation of the tail and third claw of the forelimb are secondary sexual characters in males of both species. Growth in both species progresses rapidly prior to maturity, however, *Graptemys* females seemingly grow more slowly than *Pseudemys* during this period. Rapid fluctuation of the water level may result in a slowing of growth in *Pseudemys*, but the evidence is only suggestive, not conclusive. Alternation of habitats along the shoreline due to the changing water level is believed to be responsible for the nomadic behavior of *Pseudemys* as well as in determining the quality and quantity of food available.

The abundance of the red-eared turtle, *Pseudemys scripta elegans* Wied, and the Ouachita map turtle, *Graptemys pseudogeographica ouachitensis* Cagle, in Lake Texoma, made possible a comparative life history study at the University of Oklahoma Biological Station, Marshall County, 2 miles east of Willis.

Acknowledgments.—I am grateful to Dr. Carl D. Riggs, Director of the Biological Station for permission to utilize facilities in his care. I am indebted further to Dr. Harley P. Brown of the University of Oklahoma Department of Zoology for the analysis of the animal material in the contents of digestive tracts of selected turtles, and to Dr. George J. Goodman of the University of Oklahoma Department of Botany for selected botanical determinations. Finally, thanks are extended to Drs. Fred R. Cagle and Henry S. Fitch for constructive criticism of the manuscript.

Methods

Most data were obtained from turtles trapped in hoop nets in June and July, 1954. All individuals were either marked and released or examined by dissection. Measurements were made with a millimeter rule, a Vernier caliper or with the instrument described by Cagle (1946:687). Unspecified measurements in the text refer to plastral length. Selected specimens were dissected to determine sex,

attainment of sexual maturity, reproductive potential and food habits. Ovaries and oviducal eggs as well as stomach and intestinal contents of selected specimens were removed and preserved; also, permanent slides of selected sperm smears (Wright's stain) were prepared.

In the summer of 1953, Dr. Bryan P. Glass marked turtles of several species, recording the sex and length of carapace; all were released at the shoreline just south of the Biological Station. A few of these, recovered in the summer of 1954, provided data on movement and growth. Many others were marked and released at the point of capture; data recorded included locality, sex, and plastral length. The system of marking consisted of boring a hole in a marginal plate and fastening a numbered metal tag.

Several turtles utilized in this study were collected by hand, seined, or trapped in gill nets. Most turtles were trapped in three collapsible 3-hoop nets of heavy cord or two non-collapsible metal fyke nets; the mesh-size prevented the escape of all turtles exceeding 4.0 cm. The traps, used simultaneously, were baited with freshly-chopped fish and occasionally with other meat scraps. The number of traps and traping success varied with location. Traps were moved from time to time. This trapping procedure revealed that *Pseudemys scripta* was the most abundant species. Of 156 turtles trapped from June 14 to July 12, 1954, 100 (64%) were *Pseudemys scripta,* 24 (15%) were *Graptemys pseudogeographica,* 19 (12%) were *Trionyx spinifer,* 8 (5%) were *Chelydra serpentina,* 3 (2%) were *Kinosternon subrubrum,* 1 (1%) was *Pseudemys floridana,* and 1 (1%) was *Trionyx muticus.*

The largest number of turtles trapped in a single net at any one time was 12 *Pseudemys scripta.* The nets caught specimens of *Pseudemys scripta* and *Graptemys* of all sizes and both sexes; only one adult female *Graptemys* was obtained.

Turtles of the genus *Graptemys* are considered to be partial to the deeper waters of rivers having a moderate current about emergent fallen trees, brush piles and other debris. Such habitats, which were explored during the writer's participation in Tulane University field expeditions in the summers of 1952, 1953, and 1954, yielded many specimens. Within the known geographic range of the genus, I visited a lentic habitat (Lake Concordia, Concordia Parish, Louisiana) only once. This ox-bow lake of the Mississippi River has extensive beds of submerged vegetation. Three specimens of *Graptemys kohni* were collected by hand at night in approximately four and one-half hours, employing the technique described by Chaney and Smith (1950); other individuals were seen but not collected. To my knowledge there are no published records of *Graptemys* having been collected in lentic habitats. The exploration of large ponds, lakes and impoundments undoubtedly will reveal at least some species of *Graptemys* to be more common in these situations than is currently believed.

Fig. 1.—Upper, mouth of Buncombe Creek from west bank near the Biological Station; note the barren aspect of the lake shore. Photograph taken on February 24, 1951, in a period of low water. Fig. 2.—Lower, inundated area about one mile west of the Biological Station. Photograph taken on June 19, 1951.

DESCRIPTION OF AREA

Lake Texoma was impounded in 1944 for flood control and hydroelectric power by the Denison Dam across the Red River between Grayson County, Texas, and Bryan County, Oklahoma. The conservation level or normal power pool elevation of 617 feet above mean sea level covers 93,085 acres, and the drainage basin of Lake Texoma occupies 38,291 square miles. The lake has a shoreline of approximately 650 miles and a dendritic shape; it is divided into the Red River arm separating Texas and Oklahoma, and the Washita arm that forms the boundary between Marshall and Bryan counties, Oklahoma.

The Biological Station is at the mouth of Buncombe Creek on its west bank. The surrounding area is essentially a transitional zone between the eastern blackjack-post oak forest and the western mixed grass prairie, the Osage Savannah District of Blair and Hubbell (1938:433). The marked fluctuation in water level (Figs. 1 and 2) prevents the establishment of permanent stands of aquatic vegetation in the lake; small patches of pondweed (*Potamogeton* sp.) and smartweed (*Polygonum* sp.) occur occasionally. The fluctuation of water level in the years 1949 through 1953 is presented to give some idea of the degree and rapidity of fluctuation (Fig. 3). After torrential rains, water rapidly inundates the adjacent, relatively level, areas, and often strands reptiles, and occasionally small mammals, in the boughs of willow trees. The salt cedar, *Tamarix gallica*, is often abundant when the receding water level exposes the shoreline long

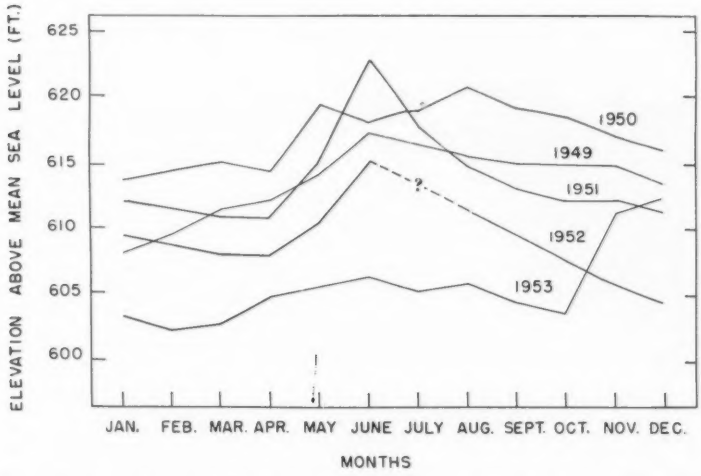

Fig. 3.—The fluctuation of water level in Lake Texoma in the years 1949 through 1953. Monthly values represent the average water levels.

enough to permit its establishment. The fogwort, *Lippia incisa,* and Bermuda grass, *Cynodon dactylon,* often dominate an extensive low cover along the shoreline; thickets of black willow, *Salix nigra,* often encroach on the lake shore. Wave action on Lake Texoma is common and often severe. The lake bottom is chiefly sand and clay, and the water is usually turbid. Basking sites for turtles, fallen trees and débris, are at a premium; tree stumps are often exposed and utilized. Sublette (1955) has commented on the physico-chemical and biological features of Lake Texoma, and Riggs and Bonn (1959) have discussed the general environmental factors and fishes. Carpenter (1955) has mentioned species of amphibians and reptiles occurring in the Lake Texoma area.

Pseudemys scripta elegans Wied

Red-eared Turtle

Of 127 individuals utilized in this study, 35 were preserved. All are in the collection of the University of Oklahoma Museum, Division of Zoology and bear the following catalogue numbers: 27131-37, 27158, 27299-300, 27307, 27314-16, 27339-42, 27388, 27555-61, 27570-72, 27577-79, 27582-83, 27595. In other parts of its range this subspecies has been the subject of intensive research by Cagle (1950).

Description.—The configuration of the red postocular blotch and the minimal size of completely melanistic males are subject to geographic variation.

Specimens having an isolated, oval, black-bordered, red blotch back of the eye, and elongated plastral blotches, which have been assumed to be indicative of intergradation with *P. s. gaigeae,* have been reported from northwestern Louisiana and central Texas (Cagle, *op. cit.*:34). The variation in configuration of the postocular blotch in specimens from southwestern Oklahoma has been mentioned by Webb and Ortenburger (1953:88). Of 120 individuals from Lake Texoma, 59 (49%) exhibit only a slight narrowing of the enlarged, red postocular blotch and have a broad bar entering the eye on both sides of the head (No. 27558). Thirty-one specimens (26%) have the smaller anterior portion of the postorbital bar clearly separated from the larger posterior section on both sides of the head (No. 27583); some of these have a dark vertical line separating the two blotches (No. 27582). Only 5 per cent of the population from northwestern Louisiana had two separate postocular red marks. The remaining 30 individuals (25%) have intermediate patterns, some possessing a narrowed anterior segment (No. 27578), others having the anterior portion constricted to the point of separation (No. 27342), and many have a combination of patterns on either side of the head (Nos. 27577, 27557). The separation of the postocular blotch from the orbit seems to be due to individual variation and not to intergradation with *P. s. gaigeae.*

Males of *Pseudemys s. elegans* become dark with an obliteration of the pattern on the soft body parts, carapace and plastron (Viosca,

1933). The assumption of melanism is not coincident with the attainment of sexual maturity. This melanism first becomes apparent on the plastron, then on the carapace and finally on the soft parts of the body. Completely melanistic individuals may have a plastron as short as 15 cm and all individuals in which it exceeds 17 cm are completely melanistic. Two of nine males in the 15.1 to 16.0 cm size-group, and one of four in the 16.1 to 17.0 cm size-group were completely melanis-

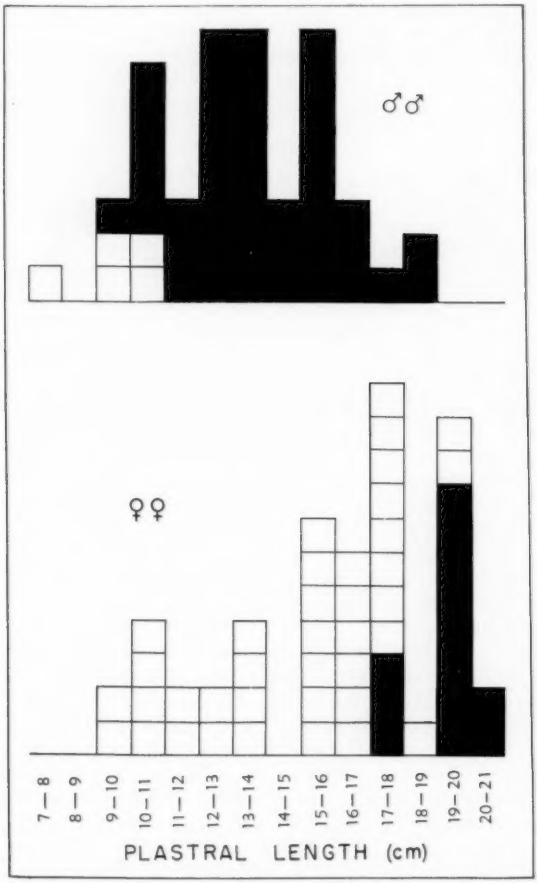

Fig. 4.—Size distribution of 98 *Pseudemys s. elegans* collected from June 17 through July 12, 1954. Open squares indicate immature individuals; solid squares indicate sexually mature individuals. Each square represents one specimen.

tic. The smallest completely melanistic male from Lake Texoma (15.2 cm) is larger than the smallest reported from eastern Texas (10 cm) or Tennessee and Illinois (13 cm) (Cagle, *loc. cit.*). Large adult females occasionally have plastrons that are as much as 80 per cent darkened.

Size at sexual maturity.—Cagle (1948:108) concludes that males become sexually mature when they reach a plastral length of 9 to 10 cm. Of 47 males, ranging in plastral length from 7.7 to 18.4 cm, 42 (89%) were sexually mature (Fig. 4). All male turtles exceeding 11.0 cm were assumed to be sexually mature on the basis of well-developed secondary sexual characters (enlarged tail and claws of forelimbs). The presence of sperm in the vasa deferentia or a portion of the testis was the criterion for sexual maturity in the remaining individuals, except two. Of the latter, one (10.7 cm) having well-developed secondary sexual characters was considered sexually mature, whereas the other (7.7 cm), was dissected and considered immature on the basis of small, undeveloped testes and vasa deferentia. The male of this species in Lake Texoma becomes sexually mature when its plastron has attained a length of 9 to 10 cm.

Some adult males differ from females of the same size in having a carapace with straight or parallel sides, that is to say, there is no curvature in the region of the bridge; this condition is accentuated by a posterior flaring of the carapace.

Cagle (1950:44) has shown that some females are sexually mature when the plastron is 15.0 cm in length; there was no apparent difference between populations from Illinois, Tennessee, and Louisiana. Of 51 female turtles ranging from 9.4 to 20.3 cm, 13 (24%) were considered sexually mature (Fig. 4). Of 22 specimens that were dissected, eight were considered sexually mature because they had oviducal eggs or corpora lutea or ovarian follicles exceeding 15 mm in diameter; these eight females included two of seven in the 17.1 to 18.0 cm size-group, four of six in the 19.1 to 20.0 size-group, and two of two in the 20.1 to 21.0 cm size-group. Five additional females, 17.5, 19.2, 19.7, 19.9 and 19.9 cm, were not dissected but were considered sexually mature on the basis of a decided cessation of growth as revealed by an examination of the growth rings. All remaining females (not dissected) showed no retardation of growth and were considered immature.

Data from four additional dissected specimens from Lake Texoma (not included in Fig. 4) are as follows: No. 27131, secured on May 19, 1951, 18.5 cm, sexually mature; No. 27299, secured on July 8, 1951, 18.0 cm, immature; No. 27300, secured on July 8, 1951, 19.3 cm, sexually mature, and a specimen taken on July 21, 1954, 18.1 cm. sexually mature.

My data indicate that some females are sexually mature when the plastron is 17.4 cm in length. Although the size of the smallest sexually mature female is unknown, the data suggest a larger size than that reported by Cagle.

Eggs.—Fifty-three oviducal eggs were 18.9 to 23.6 (mean 21.4) mm wide, and 32.6 to 39.4 (mean 37.6) mm long. The mean measurements of these eggs do not differ appreciably from corresponding measurements of oviducal eggs of populations from Illinois and Louisiana (Cagle, *op. cit.*:38). The six females containing oviducal eggs were 18.0, 19.1, 19.4, 19.9, 20.3, and 20.3 (mean 19.5) cm; the number of eggs varied from one to 12 (mean 8.8). There is no indication of a correlation of the size or number of eggs with plastral length. Counts of oviducal eggs may be biased, as in some individuals one or more eggs may have been deposited previously, or, if an extended breeding season is demonstrated and if more than one clutch per season are deposited, counts of oviducal eggs may include eggs of the previous clutch that were not deposited.

Reproductive potential.—The length of the annual breeding season for females in Lake Texoma is unknown. Whatever length it is, the breeding season is long enough for some of them to deposit three clutches as shown by individual females that contained oviducal eggs, ovarian follicles exceeding 15 mm in diameter, and corpora lutea of different sizes that exceed in number the number of oviducal eggs.

Ovarian follicles larger than 15 mm in diameter are considered to comprise, at least partly, the next clutch that will be deposited in the current season. Follicles of this size possibly are retained until the following year or some may undergo regression. Cagle (*loc. cit.*) reported follicles exceeding 10 mm in diameter in females examined in September and October from Louisiana and Illinois.

The different sizes of the corpora lutea that exceed in number the number of oviducal eggs suggest that a clutch had previously been deposited in the same season (year). The maximum diameter of the largest corpora lutea, which represent ovulation points of eggs contained in the oviducts, is 8 to 9 mm. The maximum diameter of the largest corpora lutea in turtles that contained no oviducal eggs, collected in the breeding season, is 5 to 6 mm. The length of time that the eggs remain in the oviduct, and the length of time between their deposition and ovulation of the succeeding clutch is unknown. The corpora lutea presumably decrease at least 3 to 4 mm in diameter between ovulation and deposition and perhaps more between successive ovulations. Assuming an equal and continuous rate of regression of all corpora lutea, those representing ovulation points of the last clutch of the breeding season probably regress to corpora albicantia by the beginning of the next annual breeding season. Risley (1933:694) states that the eggs of *Sternothaerus odoratus* remain in the oviducts for a period of from 20 to 35 days. If the eggs of *Pseudemys s. elegans* remain in the oviduct for this length of time, corpora lutea probably regress completely (about three mm every 27 days) in approximately three months. Edgren (1960:61), however, writes that the life of the egg in the oviduct of *S. odoratus* must be between five and eight weeks.

Follicles of the most enlarged groups in the ovaries of each of the 11 sexually mature females varied in extremes from 10 to 21 mm in

diameter. Counts of these follicles indicated an average reproductive potential of 16.2 eggs per clutch, which is almost twice the 8.8 revealed by counts of oviducal eggs. This discrepancy is due to the inadvertent inclusion of developing follicles that are not representative of the succeeding egg complement; also, some may remain unfertilized and others may become atretic. Follicles considered atretic are red-brown; the color is darker in the smaller follicles. The largest follicle considered to be undergoing atresia was 12 mm in diameter and a pale red-brown, contrasting with the yellow-orange of the viable follicles.

All 11 females, collected from May 19 to July 21, contained ovarian follicles 15 mm in diameter or larger. Five of seven specimens collected in June contained oviducal eggs, whereas one of three collected in July contained one egg in the oviduct. The presence of one oviducal egg on July 12 in a female having no corpora lutea indicates retention of this egg for a considerable length of time (equal to that necessary for complete regression of the corpora lutea), and presumably the egg was a remnant of a previous deposition. The two females collected on July 8 and May 19, which had no oviducal eggs or corpora lutea to indicate recent deposition, but possessed follicles 14 to 17 mm in diameter, suggest the approach of the first ovulation for the current breeding season; these females may or may not be in their first reproductive season. The collection date of July 8 suggests that the first clutch of a season need not be deposited at the beginning of the breeding season, and that a female may deposit only one clutch per season, whereas other females may deposit two or three.

Lake Texoma females are apparently capable of depositing three clutches per season. The deposition of repeated clutches in a long egg-laying season has been mentioned for *Chrysemys* (Cagle, 1954:229) and other turtle species (Cagle, 1950:38). The total annual reproductive capacity of some females may amount to 36 eggs (maximum of 12 per clutch; maximum of 3 clutches per season), but the realized annual reproductive capacity is estimated to be approximately 26.4 eggs (mean of 8.8 per clutch; maximum of 3 clutches per season).

Growth.—The estimate of growth is based on calculated increments from measurements of growth rings, which has been shown to be valid for *Pseudemys s. elegans* (Cagle, 1946).

The calculated plastral length of 26 individuals at hatching was 2.3 to 3.9 (mean 3.1) cm; of these eight were males, 2.6 to 3.8 (mean 3.1) cm, and 18 were females, 2.3 to 3.9 (mean 3.1) cm. At the end of the first year of growth (the first growing season) seven males were 4.1 to 6.3 (mean 5.4) cm, and had increased 1.5 to 3.2 (mean 2.2) cm; 18 females were 4.2 to 7.8 (mean 6.2) cm, and had increased 1.7 to 4.7 (mean 3.1) cm. At the end of the second year of growth, six males were 6.0 to 8.3 (mean 7.1) cm, and had increased 1.2 to 2.7 (mean 1.9) cm; 12 females were 6.2 to 11.3 (mean 9.1) cm, and had increased 0.9 to 4.5 (mean 2.8) cm. At the end of the third year of growth, four males were 7.4 to 10.9 (mean 8.9) cm, and had increased

0.8 to 2.7 (mean 1.2) cm; seven females were 8.0 to 14.0 (mean 11.4) cm, and had increased 0.9 to 3.5 (mean 2.2) cm. The ring bordering the femoral plate at hatching in 26 turtles examined was still evident in three females that had rings representing the termination of growth

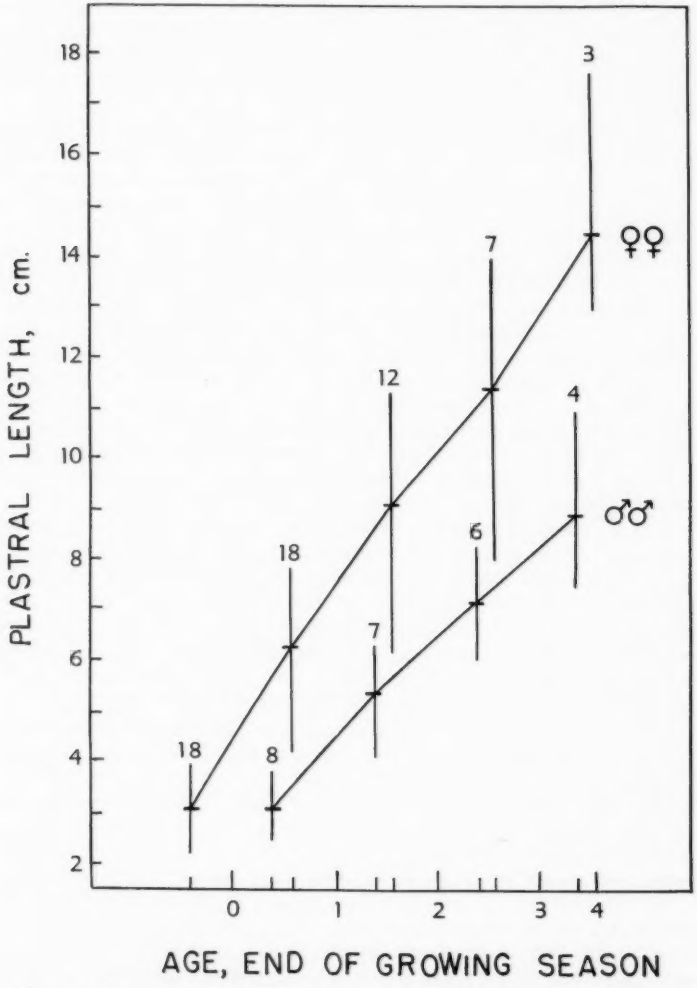

Fig. 5.—Early growth of *Pseudemys s. elegans*. Vertical lines indicate the range in length of plastron; the diagonal lines connect the means. The figure above each line represents the number of specimens.

in the fourth year; these indicated a size of 12.9 to 17.6 (mean 14.5) cm, and had increased 1.3 to 3.8 (mean 2.6) cm. A growth curve is plotted from the calculated plastral lengths for these individuals (Fig. 5). Thus, some males become mature in their third year (one, 10.9 cm, No. 27133), and females in their fourth (one, 17.6 cm, No. 27560). Growth is seemingly more rapid and variable in females. The variation in growth is attributed to individual variation, to the inclusion of individuals that are representative of clutches deposited at different times in the same breeding season, and to those whose seasonal increments of increase occurred in different growing seasons.

Segments of the growth curve were calculated for 38 males and 42 females in which the ring bordering the femoral plate at hatching was not evident and thus the age was unknown. These growth segments were assigned to arbitrary size-groups in each growing season and the average increments of increase within each size-group determined (Table I). Despite apparent exceptions owing to individual variation or lack of specimens, the general tendency is a slowing trend of growth with larger size in both sexes, the greatest retardation occurring at the size of attainment of sexual maturity. The largest increments of increase for any individuals were those of a male that increased 6.1 (4.1 to 10.2) cm in the growing season of 1952, and a female (No. 27131) that increased 5.2 (7.4 to 12.6) cm in the growing season of 1949.

Data on growth for five recaptured individuals are presented in Table II. All three males were sexually mature. Two females, both immature, showed relatively the largest increments of increase.

Analysis of growth as affected by varying ecological factors is difficult because of extreme variation with sex and size. However, variation in growth for the population here studied is probably correlated with the fluctuation in water level. In the growing season of 1953 six immature males increased an average of only 0.9 cm (Table I), whereas the average increment of increase for males in the same general size-group in other growing seasons exceeded 2.1 cm. Two immature females in the growing season of 1953 increased an average of 1.4 cm, whereas those in the same general size-groups in other growing seasons (except possibly 1952) exceeded an average of 2.6 cm. An examination of Figure 3 reveals that the lowest elevation of water level occurred most consistently in 1953. Possibly a lowering of the water level for a significant length of time decreases the availability of the food supply, which in turn, retards growth. However, the increments for the other size-groups of immature females in the growing season of 1953 are not noticeably retarded as one would expect; possibly only certain-sized individuals are affected. The arbitrary selection of size-groups, which overlap within each growing season and are not exactly comparable between growing seasons, obscures an evaluation of size-group comparisons. Although suggestive, these data do not clearly demonstrate that water fluctuation is a factor influencing growth rate.

Food.—Presumably a direct influence of fluctuation of water-level is on the food supply, but omnivorous habits (Cagle, 1950:48) allow

TABLE I.—Growth rates in *Pseudemys scripta elegans* of different size groups in different growing seasons

Year	Average extremes in plastron length of turtles at the beginning and end of growing season (cm)	Number of increments in sample	Average increment of increase in plastron length (cm)
	Males (38)		
1949	7.5-10.3	1	2.8
1950	4.4-6.6	1	2.2
	7.7-9.2	1	1.5
	10.4-12.2	2	1.8
	16.5-16.9	1	0.4
1951	6.0-8.9	2	2.9
	9.0-11.1	5	2.1
	13.3-14.5	1	1.2
1952	6.4-9.2	5	2.8
	10.6-11.8	10	1.2
	12.3-13.0	2	0.7
	14.2-14.6	2	0.4
1953	8.7-9.6	6	0.9
	10.7-11.9	7	1.2
	11.8-12.7	5	0.9
	12.8-13.6	8	0.8
	14.5-15.2	8	0.7
	Females (42)		
1949	4.0-7.3	1	3.3
	7.2-10.2	5	3.0
	12.1-15.6	1	3.5
	14.9-18.7	1	3.8
1950	5.5-8.2	5	2.7
	8.0-10.6	4	2.6
	10.2-13.3	3	3.1
	12.5-16.1	2	3.6
	15.6-18.0	1	2.4
	18.7-19.1	1	0.4
1951	5.2-7.8	1	2.6
	8.6-11.3	13	2.7
	12.3-13.6	2	1.3
	14.1-16.2	6	2.1
	17.2-18.1	3	0.9
1952	6.9-10.0	4	3.1
	11.6-13.0	16	1.4
	13.8-15.2	6	1.4
	17.0-18.2	8	1.2
1953	6.2-9.5	2	3.3
	10.5-11.9	2	1.4
	12.6-14.7	19	2.1
	15.6-17.2	9	1.6
	17.5-19.0	1	1.5
	18.8-19.3	6	0.5

this species to thrive in areas subject to an alternating availability of different food supplies. Individuals have been observed feeding on insects, fish and other vertebrate remains in captivity. In a period of inundation, the stomach and intestine of two females (15.1 and 15.6 cm) collected on June 21, 1954, and one female (20.3 cm) taken on July 12, 1954, were extended with large quantities of the herb, *Lippia incisa*. One specimen, showing no apparent ill effects when alive, had the barbed end of a small fish hook protruding from the stomach.

Movement.—Information concerning the extent of movement is based on the distance between points of release and capture for four recaptured turtles. One male, bearing metal tag number 4230, had moved a distance of approximately one and one-half miles from July 23, 1953, to July 21, 1954, whereas the female, No. 127, moved about one-third of a mile from sometime in July, 1953, to June 22, 1954. Another male, No. 4213, had moved approximately one mile from July 20, 1953, to June 21, 1954. The other male, No. 4241, which had moved about two-thirds of a mile from July 23, 1953 to June 18, 1954, was recaptured on June 20, 1954, and had moved about the same distance in this two-day period. Data obtained by Cagle (1944:18) for this subspecies in southern Illinois suggest that each turtle tends to remain within one area of a body of water. My data indicate much movement, but the marked turtles were not initially released at the site of original capture and may have made homing movements in some instances. However, the recaptured male, No. 4241, traveled approximately two-thirds of a mile in two days after being released at the site of capture.

A nomadic behavior is suggested and is perhaps stimulated by the change in habitat and morphometry due to the rapid fluctuation in water level; this change possibly prevents the recognition of any localized habitat, and the consequent establishment of a home range. Cagle (*op. cit.*:27) suggested that the transfer of individuals of *Chrysemys* to a strange habitat effects a nomadic behavior.

Graptemys pseudogeographica ouachitensis Cagle

Ouachita Map Turtle

Of 49 turtles utilized in this study, 37 were preserved and bear the following catalogue numbers: University of Oklahoma Museum, Divi-

TABLE II.—Growth of five recaptured *Pseudemys scripta elegans*

Number on metal tag	sex	carapace length (cm) release		recovery		increment of increase (cm)
102	female	Jun. 18, '53	7.1	Jul. 16, '53	7.9	0.8
127	female	Jul. ?, '53	8.7	Jun. 22, '54	13.1	4.4
4213	male	Jul. 20, '53	13.4	Jun. 21, '54	15.1	1.6
4230	male	Jul. 23, '53	12.2	Jul. 21, '54	14.4	2.2
4241	male	Jul. 23, '53	12.9	Jun. 18, '54	13.8	0.9
		Jun. 18, '54	13.8	Dec. 18, '55	15.6	1.8

sion of Zoology (UOMZ) 26911-12, 27130, 27327, 27551-54, 27564-65, 27567-68, 27573-76, 27580-81, 27584-92; University of Kansas Museum of Natural History (KU) 40167-74, skeletons have since been prepared of these specimens; Tulane University (TU) 16661-.1, 17300-.1. This material affords hitherto unrecorded information concerning aspects of the species' natural history as well as descriptive comments to augment our knowledge of geographic variation.

Description.—Turtles of this subspecies from Lake Texoma differ in certain respects from the type description (Cagle, 1953:15), and their brief description here will serve to supplement that by Carr (1952:211) based on specimens from Medicine Creek, Comanche County, Oklahoma.

The measurements (in cm) of two hatchlings (TU 17300-.1) in their first year of growth are, respectively, as follows: length of carapace 4.0, 4.7; width of carapace 3.7, 4.3; height of carapace 1.8, 2.0; length of plastron 3.6, 4.1; width of head 0.9, 0.9. There are 37 and 43 longitudinal light stripes on the neck, 10 and 11 on the anterior surface of the forelimb, and 11 and 13 on the upper surface of the hindlimb. The postocular blotch is oblong and smaller than (two-thirds to three-fourths) the height of the orbit; the blotch is not in contact with the upper longitudinal light stripes in TU 17300 but narrowly in contact anteriorly in TU 17300.1. Eight light longitudinal neck stripes (3 wide stripes flanked by 5 narrower stripes) enter the orbit. The lateral yellow spots on the ventral surface of the lower jaw may be nearly circular like the central spot or more elongate. The marbled plastral pattern, more concentrated than that figured by Cagle (*op. cit.*:15, fig. 3B), is more or less symmetrical and comprises an estimated three-fourths of the plastral area. The bridge and undersurface of the marginals are extensively dark-marked, and the black of the knobs on the first, third and fourth vertebrals is less extensive than that figured by Cagle (*op. cit.*:13, fig. 2A).

The head is not conspicuously broadened in nine adult females. The length of plastron (15.4 to 17.0, mean 16.2 cm) is 6.8 to 7.6 (mean 7.1) times the width of the head (2.2 to 2.4, mean 2.3 cm). The size of head cannot be compared with that reported by Cagle (*op. cit.*:14) because width of carapace was not recorded by me.

A feature of coloration (in life) of adult males and females is not mentioned by Cagle. The network of light lines on the carapace, the wide circular marks on the ventral surface of the marginals, and especially the dorsal and lateral neck stripes are orange (not yellow). Occasional individuals of *G. kohni,* and *G. p. ouachitensis* in other parts of its range, may possess the orange striping on head and neck, but it is not a consistent feature of the population. A kyphotic specimen from Marshall County has been mentioned by Carpenter (1958: 116). The photographs of two adult females (Fig. 6) illustrate the habitus of specimens from Lake Texoma.

Some of the variation noted above has been mentioned by Cagle (*op. cit.*:15). Briefly, the population in Lake Texoma differs from

the type description in 1) the larger number of stripes on the neck, anterior surface of the forelimb, and upper surface of the hindlimb; 2) the usually isolated, oblong, postorbital blotch that is smaller than the height of the orbit; 3) the larger number of stripes that enter the orbit; 4) the extensive plastral pattern in hatchlings; 5) the reduction of black on the vertebral knobs in hatchlings, and 6) the orange striping.

Size distribution.—Of 24 females (all collected within a 24-day period in mid-summer) there is a decided prominence of immatures (Fig. 7). This contrast in size distribution of female *Graptemys* and *Pseudemys* (see Fig. 4) reflects the different food habits of the two species and the collecting method used. Large adult females of *Graptemys* are seldom seen, and then are extremely wary and difficult to catch. The majority of the adult female *Graptemys* used in this study were obtained from gill nets or seined from shallow areas.

Size at sexual maturity.—Cagle (*op. cit.*:12) lists the extremes in size of adult males as 7.8 and 9.2 cm; his criteria for sexual maturity are presumably the elongation of the nails of the forefeet (*op cit.*:14) and the enlargement of the tail. Of 13 males from Lake Texoma with extremes of 4.4 and 8.7 cm, nine were sexually mature; the smallest mature one was 7.3 cm. Only six males were dissected and the testes smeared for the presence of sperm; five, which had pigmented vasa deferentia, were adult (7.5, 7.8, 8.3, 8.3, and 8.5 cm), and one was immature. Four other males (7.3, 7.7, 8.4 and 8.7 cm) were considered mature on the basis of well-developed secondary sex characters. This suggests a plastral length of approximately 7.0 cm as the size of attainment of sexual maturity. The marked change in the relation of length of tail to length of plastron in males at the size of attainment of sexual maturity has been clearly demonstrated for *Pseudemys s. elegans* (Cagle, 1948:108), *Chrysemys picta* (Cagle, 1954:232), and *Trionyx spinifer emoryi* (Webb, 1956:121), and is apparent in adult males of other species of turtles. Figure 8A reveals an increase in length of tail as male specimens of *Graptemys* reach a size of 7.0 cm. The cloacal opening extends beyond the posterior edge of the carapace in adult

Fig. 6.—Adult females of *Graptemys p. ouachitensis;* both have plastron lengths of 16.7 cm. Left, KU 40171; right, UOMZ 27581.

males; the distance measured was from the rear edge of the carapace to the anterior lip of the cloaca. Cagle (1948:108) has also shown the length of the claws of the forelimb to be a secondary sex character in *P. s. elegans* as well as in male *Chrysemys* (1954:232). Male specimens of *G. p. ouachitensis* also show a decided lengthening of the third claw of the forelimb (measured in a straight line from its base to tip) when a plastral length of 7.0 cm is attained (Fig. 8B). Only one sexually mature male (testis smeared) had not developed a lengthened third claw. Male turtles become sexually mature when they reach a plastral length of approximately 7.0 cm, and the lengthening of tail and third claw of the forelimb are secondary sex characters.

Two adult females, 15.4 and 15.5 cm, were available to Cagle (1953:14). Of 35 females ranging from 4.1 to 17.0 cm, nine were considered sexually mature; the smallest one was 15.4 cm. All females (14) exceeding 12.5 cm were examined by dissection. Three, of four obtained in 1954 and dissected at the time of collection, had pigmented oviducts and were considered sexually mature; two (16.6 and 16.7 cm) had oviducal eggs, and the other (16.0 cm) had ovarian follicles 16.5 to 22.6 mm in diameter. The immature female (14.0 cm) captured in 1954 possessed unswollen oviducts 3 mm wide, and compact ovaries having the largest follicles 3 mm in diameter. Two immature females (13.1 and 14.9 cm) collected on June 30, 1949, and July 11, 1951, respectively, had ovaries that contained follicles 2 to 3 mm in diameter.

Eight females collected in the summer of 1955 (no exact date) were transported to the University of Kansas and not preserved there until early June, 1956. Of these, two females (12.7 and 15.3 cm), considered immature, had compact ovaries in which the largest ovocytes were 2 mm in diameter; the oviducts, slightly pigmented posteriorly, were 2 to 3 mm wide in the smaller specimen, and 6 mm wide in the larger turtle. Six females (15.4 to 17.0 cm), considered sexually mature, had swollen convoluted oviducts 7 to 10 mm wide; the ovaries contained red bodies (corpora lutea or atretic follicles) not exceeding 4 mm in diameter, and the largest follicles were 3 to 5 mm in diameter. The posterior portions of the oviducts were nearly a uniform black. Although the definition of the size at sexual maturity is somewhat difficult to make by assaying the latter specimens, which are in a period of sexual inactivity, the two specimens, 14.9 cm (UOMZ 26911, immature) and 16.0 cm (UOMZ 27580, mature) indicate that females of *G. p. ouachitensis* in Lake Texoma are sexually mature when the plastron has attained a length of from 15.0 to 16.0 cm.

Eggs.—Only two of nine adult females contained eggs in their oviducts. One turtle, 16.6 cm and obtained on July 6, contained seven eggs (four in the left oviduct), which measured 22.2 to 23.8 (mean 23.2) mm in width, and 32.8 to 35.9 (mean 34.7) mm in length. A female (UOMZ 27581), 16.7 cm and captured on June 21, contained six oviducal eggs (four in the left oviduct), which measured 18.7 to 22.0 (mean 20.4) mm in width and 36.5 to 40.3 (mean 38.5) mm in length. The four eggs in the left oviduct from the turtle taken on June

21 were not turgid, but soft and crowded with creases in their walls; these eggs were noticeably more elongate and the measurements more variable than those of the other eggs. The two complements of oviducal eggs indicate a mean of 6.5.

Reproductive potential.—An analysis of the reproductive potential is limited to information obtained from an examination of three females. One, 16.6 cm and obtained on July 6, contained seven oviducal eggs. Her ovaries contained three follicles that ranged from 18.7 to 19.5 mm in diameter, and two, 14.4 to 15.4 mm; seven corpora lutea ranged from 8 to 9 mm in diameter, and six, 4 to 6 mm. Another female (UOMZ 27580), 16.0 cm and obtained on June 21, contained no oviducal eggs but the ovaries possessed five corpora lutea 8 mm in diameter and 26 enlarged follicles (10 were 16.5 to 22.6 mm, and 16 were 9.5 to 15.3 mm in diameter). The third specimen (UOMZ 27581), 16.7 cm and captured on June 21, contained six oviducal

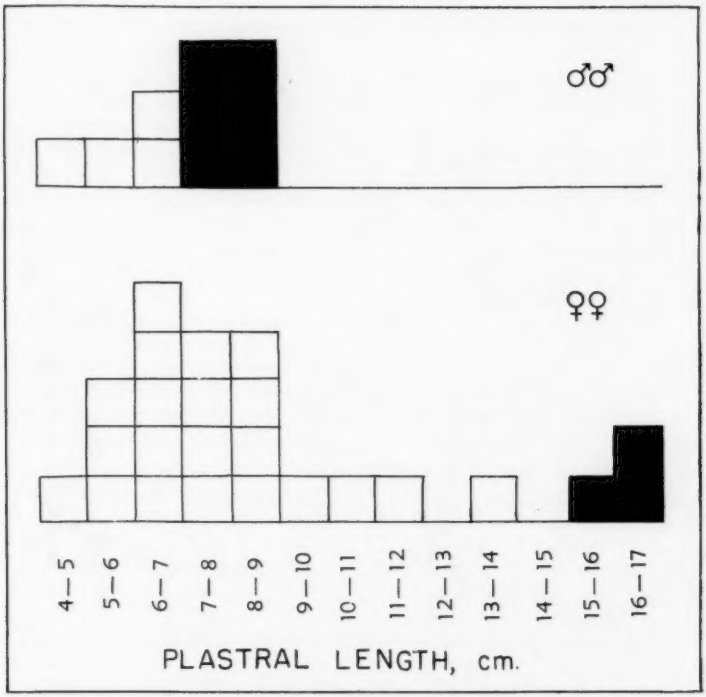

Fig. 7.—Size distribution of 34 *Graptemys p. ouachitensis* collected from June 13 through July 6, 1954. Open squares indicate immature individuals; solid squares indicate sexually mature individuals. Each square represents one specimen.

eggs. Her ovaries contained four follicles that ranged from 18.0 to 23.3 mm in diameter and five, 11.8 to 15.2 mm; six corpora lutea ranged from 8 to 9 mm in diameter, and eight, 4 to 7 mm.

The data suggest that, as in the Lake Texoma population of *P. s. elegans*, three clutches of eggs are laid in one season of sexual activity. This is evidenced by the possession of corpora lutea approximately 9 mm in diameter that are taken to represent the ovulation points of those eggs contained in the oviducts or those recently deposited (UOMZ 27580). The set of smaller-sized corpora lutea are indicative of an earlier clutch in the same season, and the enlarged groups of follicles (exceeding 15 mm in diameter) are suggestive of a subsequent egg complement to be deposited in the same reproductive season.

The ovaries of the females considered to be sexually inactive, contained follicles that did not exceed 5 mm in diameter and possibly corpora lutea not exceeding 4 mm in diameter, although the latter were not certainly distinguished from atretic follicles. A large corpus

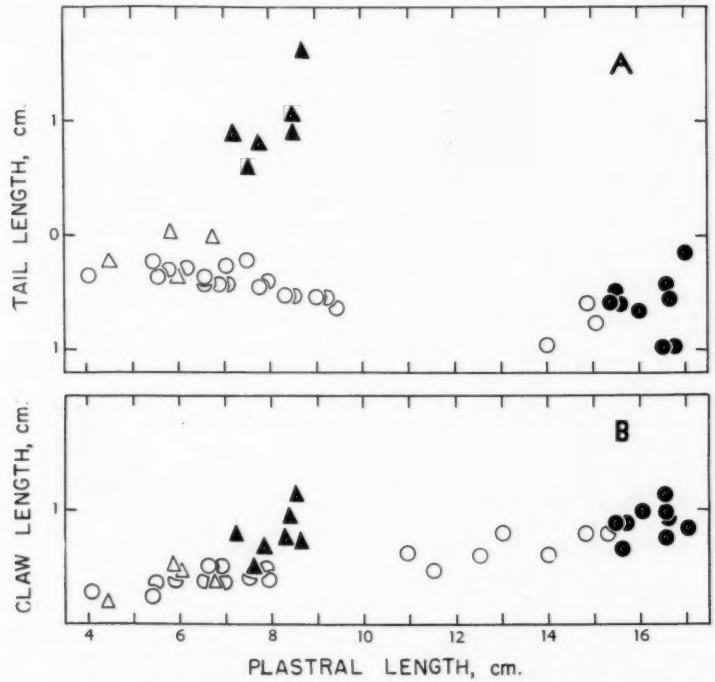

Fig. 8.—The relation of length of tail (A) and third claw of forelimb (B) to plastral length in *Graptemys p. ouachitensis*. Triangles indicate males and the circles females; solid symbols indicate sexually mature specimens, and open symbols immature specimens.

luteum (8 to 9 mm) is pale with red borders having a clearly-visible point of rupture, and is easily distinguished from an atretic follicle of the same or somewhat smaller size. The small size of the follicles in large sexually mature females, which were opened in early June at a time when much larger follicles are to be expected suggests that the environmental conditions to which the Kansas specimens were subjected in captivity were abnormal. Seemingly, ovarian follicles of a size at least 5 mm in diameter are contained in sexually inactive females. The abnormal conditions also may have prevented the complete regression of the corpora lutea; however, sexually inactive, females may contain corpora lutea approximately 4 mm in diameter.

It is assumed, then, that the largest set of follicles (exceeding 15 mm) are ovulated the same breeding season and corpora lutea of a size-group 4 to 7 mm represent ovulation points of an earlier clutch in the same reproductive season. Using only the most enlarged sets of follicles as a basis for an estimate of the reproductive potential, counts of 3, 10 and 4 indicate an average of 5.7 as compared with the realized oviducal egg count of 6.5.

The data suggest an annual reproductive capacity of at least 21 eggs (maximum of 7 per clutch; maximum of 3 clutches per season), and a realized annual reproductive capacity for each female of 19.5 eggs (mean of 6.5 per clutch; maximum of 3 clutches per season).

Growth. — Data derived from 28 turtles one to three years old indicate that measurement of growth rings are adequate for determining the length the plastron increases each year. This procedure assumes that, as in *Pseudemys s. elegans,* there is one annual growing season. Ideally a comparison of plastron lengths calculated from measurements of growth rings with those of hatchlings in which no growth has occurred is desirable. However, there is no difference in the mean plastral lengths of four hatchlings, which had not completed their first year of growth (2.8 to 3.1, mean 2.9 cm), and 24 turtles which either had completed their second or third or were in their fourth year of growth (2.2 to 3.4, mean 2.9 cm); measurements were calculated from growth rings of the femoral plate.

The calculated plastral length of 28 individuals at hatching was 2.2 to 3.4 (mean 2.9) cm, of which (two were not sexed) seven were males, 2.6 to 3.2 (mean 3.0) cm, and 19 were females, 2.2 to 3.4 (mean 2.9) cm. At the end of the first year of growth six males were 4.8 to 5.3 (mean 5.0) cm, and had increased 1.6 to 2.6 (mean 2.1) cm; 17 females were 3.6 to 6.0 (mean 5.0) cm, and had increased 0.7 to 3.5 (mean 2.0) cm. At the end of the second year of growth two males were 6.3 to 7.3 (mean 6.8) cm and had increased 1.1 to 2.4 (mean 1.8) cm; eight females were 6.0 to 8.1 (mean 7.1) cm, and had increased 1.4 to 2.6 (mean 2.0) cm. Of 23 turtles used in determining the growth rate, only one female, which had completed its third year of growth, still had the growth ring at hatching evident; this individual was 9.5 cm and increased 2.3 cm in its third year. A growth curve is plotted from the calculated plastral lengths

for these individuals (Fig. 9). Thus, some males become sexually mature in their second year (one, 7.3 cm). Assuming an average increase in females of 2.0 cm for each year (as indicated for the first two years), females do not become sexually mature until their sixth or seventh year. The rate of growth is approximately equal in both sexes during the first two years but more variable in females.

One hatchling, which had a calculated plastral length at hatching of 3.1 cm, increased only 0.5 cm when examined at the time of collection, June 16, 1954 (3.6 cm), whereas another having a calculated plastral length of 2.8 cm at hatching had increased 1.4 cm when

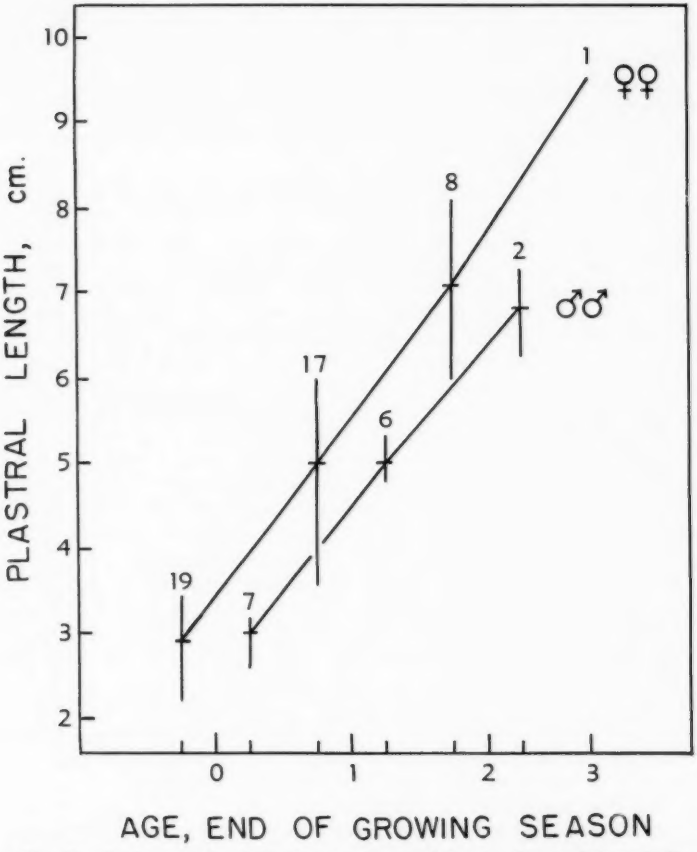

Fig. 9.—Early growth of *Graptemys p. ouachitensis*. Vertical lines indicate the range in length of plastron; the diagonal lines connect the means. The figure above each line represents the number of specimens.

captured on June 17, 1954 (4.2 cm). This variation in rate of growth is also evident in females following their first year of growth (extremes in increase in length of plastron, 0.7 to 3.5 cm), and suggests the inclusion of individuals that are from clutches deposited at different times in the same breeding season. Presumably those turtles with small increments of increase are from clutches deposited late in the breeding sason.

Five turtles that had the birth plate of the hatchling no longer evident, and whose age was therefore not definitely known, provide further data on the rate of growth. A sexually mature male (7.8 cm) when captured in the growing season of 1954, had calculated plastron lengths of 7.5, 7.1, 6.6 and 5.6 cm at the termination of the successive preceding growing season. Thus, there is a slowing of growth as the size at sexual maturity is attained; assuming the length of 5.6 cm to represent the size at the end of the first year of growth (see Fig. 8), this individual became sexually mature in its third year. Four immature females, 11.5, 13.1, 14.0 and 14.9 cm, showed variable and relatively rapid growth, the average increment of increase (combining those of different growing seasons) being 2.1 cm (extremes 0.9 to 3.7). The smallest increment, 0.9 cm, which occurred in the largest female (14.9 cm when obtained in the growing season of 1952), represented its last complete season of growth, and suggests the onset of sexual maturity. These data indicate that females grow rapidly prior to the attainment of sexual maturity (their first five to six years).

Food. — The stomach contents of eight immature *Graptemys* were analyzed qualitatively as completely as possible. Two males and six females, in which the length of the plastron ranged from 5.4 to 7.9 cm, were collected in the period June 17 to 19, inclusive. There was no indication that males and females differed in their food preferences.

A predominantly insectivorous diet was indicated in which midge larvae, ants and caddisworms (with cases of sand grains) were the most abundant items of food; small hemipterans were the next most frequent. Large portions of a bryozoan colony occurred in the stomach of one female. Small amounts of a filamentous alga and other plant fragments were perhaps ingested incidental to other food. The bulk of the contents in two specimens was composed of flesh, presumably fish, that was used for baiting the turtle traps. Numerous nematodes, four small flukes and a tapeworm from the intestines were also recorded. Other items identified include the remains of a crawfish, one cricket, one adult dragonfly and damselfly, one ephemeropteran naiad, one adult vespid wasp, two orb-weaver spiders, and coleopterans comprising three adult carabids, four dytiscid larvae and one elaterid larva.

The stomach of an adult female, 16.6 cm and drowned in a gill net on July 6, was gorged with grasshoppers. Another adult female, obtained in a fyke net on June 21, had an abundance of Bermuda grass (*Cynodon dactylon*) and fogwort (*Lippia incisa*) in the stomach.

The smaller individuals seem to prefer insects; this preference probably persists in the larger turtles. The feeding habits of this map turtle in Lake Texoma are perhaps best regarded as omnivorous in view of the presence of vegetable matter and carrion (fish). The presence of fish in the stomach contents suggests a purposeful entrance of the turtles into the traps. The diet is probably determined by the food supply available; this may vary seasonally and be largely influenced by the fluctuating water level.

REFERENCES

BLAIR, W. F. AND T. H. HUBBELL 1938. The biotic districts of Oklahoma. *Am. Midl. Nat.*, **20**(2):425-454.

CAGLE, F. R. 1944. Home range, homing behavior and migration in turtles. *Misc. Publ. Mus. Zool., Univ. Mich.*, 61:1-33.

———1946. The growth of the slider turtle, *Pseudemys scripta elegans*. *Am. Midl. Nat.*, **36**(3):685-729.

———1948. Sexual maturity in the male turtle, *Pseudemys scripta troosti*. *Copeia*, **1948**(2):108-111.

———1950. The life history of the slider turtle, *Pseudemys scripta troostii* (Holbrook). *Ecol. Monogr.*, **20**:31-54.

———1953. Two new subspecies of *Graptemys pseudogeographica*. *Occas. Pap. Mus. Zool., Univ. Mich.*, 546:1-17.

———1954. Observations on the life cycles of painted turtles (genus Chrysemys). *Am. Midl. Nat.*, **52**(1):225-235.

CARPENTER, C. C. 1955. The amphibians and reptiles of the University of Oklahoma Biological Station area in south central Oklahoma. *Proc. Okla. Acad. Sci.*, **36**:39-46.

———1958. An unusual Ouachita map turtle *Herpetologica*, **14**:116.

CARR, A. F. 1952. Handbook of Turtles. Comstock Publishing Co., Ithaca, N. Y.

CHANEY, A. H. AND C. C. SMITH 1950. Methods for collecting map turtles. *Copeia*, **1950**(4):323-324.

EDGREN, R. A. 1960. Ovulation time in the musk turtle, *Sternothaerus odoratus*. *Ibid.*, **1960**(1):60-61.

RIGGS, C. D. AND E. W. BONN 1959. An annotated list of the fishes of Lake Texoma, Oklahoma and Texas. *Southwestern Nat.*, **4**(4):157-168.

RISLEY, P. L. 1933. Observations on the natural history of the common musk turtle, *Sternotherus odoratus* (Latreille). *Pap. Mich. Acad. Sci., Arts, Letters*, **17**:685-711.

SUBLETTE, J. E. 1955. The physico-chemical and biological features of Lake Texoma (Denison Reservoir), Oklahoma and Texas: A preliminary study. *Texas J. Sci.*, **7**(2):164-182.

VIOSCA, P. 1933. The *Pseudemys troostii-elegans* complex; a case of sexual dimorphism. *Copeia*, **1933**(4):208-210.

WEBB, R. G. 1956. Size at sexual maturity in the male softshell turtle, *Trionyx ferox emoryi*. *Ibid.*, **1956**(2):121-122.

——— AND A. I. ORTENBURGER 1953. Reptiles of the Wichita Mountains Wildlife Refuge, Comanche County, Oklahoma. *Proc. Okla. Acad. Sci.*, **34**:87-92.

Additional New Species in the Genus Priocnessus Banks (Hymenoptera: Psammocharide) with Photomicrographs of Genitalia of All the New Males

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ABSTRACT: Seven new species of the genus *Priocnessus* (Hymenoptera: Psammocharidae) are described. Known only from males are *P. evansi, P. ruficrus,* and *P. bicuspidus.* Descriptions based on females only include *P. hirsutus, P. nigropectus, P. tridentatus* and *P. grandis.* Both sexes are described for *P. spinosus.* The previously undescribed male of *P. hurdi* Dreisbach is treated. *P. cincticornis* (Cresson) and *P. orbiculatus* (Smith) are considered as distinct species and the males and females are redescribed. Photomicrographs of the genitalia of all new males and revised keys to the known neotropical species are presented.

In a previous paper (Dreisbach, 1960), I described seventeen new species of the genus *Priocnessus,* and presented keys to all known neotropical species.

A recently acquired collection contains seven undescribed species, males of *P. hurdi* previously known only from females, and additional individuals of *P. rubrus* and *P. niger.* This material was made available to me by Dr. H. E. Evans, who collected specimens on his recent trip to Mexico and who had secured other specimens from other collections.

In working up these specimens I have come to the conclusion that P. *cincticornis* (Cresson) and P. *orbiculatus* (Smith) are not the same species. Dr. H. K. Townes compared a male collected by myself in Mexico to Smith's type in the British Museum. The male matched the type of *P. orbiculatus* perfectly. This specimen has a black abdomen with large yellowish spots on the sides of the tergite while Cresson (1867) described *cincticornis* as having a yellowish-ferruginous abdomen; Cresson's type is a female and it does not seem logical that the male would have a black abdomen since males are normally more highly maculated and brighter colored than the females. The male of *orbiculatus* has the last three joints of antennae flattened and larger than the preceding joints. The posterior trochanter has a small ventral tooth at the apex. It is impossible to know whether the male of *cincticornis* would have these characters.

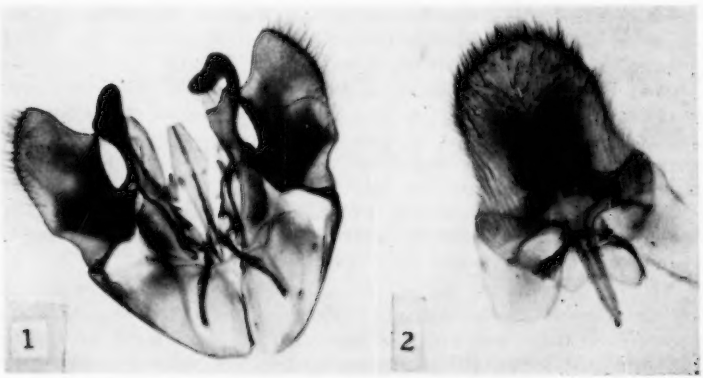
In the descriptions below, the numbers in parenthesis which follow the "lower" or "upper interocular distance" refer to the relative distance on the same scale as the ratio of the lengths of the first four antennal joints. All photomicrographs are from a magnification × 25.

The designations for deposit of the type specimens in this paper are as follows: Am. Mus. = American Museum, New York City, New York; ANSP = Academy of Natural Sciences, Philadelphia, Pennsylvania; HAS = H. A. Scullen, Oregon State College, Corvallis, Oregon; CU = Cornell University, Ithaca, New York; PDH = Paul D. Hurd, Jr., Dept. of Entomology, University of California, Berkeley 4, California; RRD = R. R. Dreisbach, Midland, Michigan; and USNM = U. S. National Museum, Washington, D. C.

Priocnessus evansi n. sp.

Figs. 1 and 2

Holotype Male.—Insect mostly black, marked with color as noted; clypeus, face, front from inner orbits to antennae (narrowing to a point just opposite anterior ocellus), posterior orbits broadly, and middle of mandibles, whitish to yellowish; lower front corners of pronotum across lower edge and continuing upward and across posterior edge of pronotum, reddish yellow; all of the legs rufous beyond trochanters except last three joints of posterior tarsi, and blackish tips of coxae; most of trochanters also rufous; underside of antennae rufous, upper side black; tegula and base of wing rufous, about 3.0 × the length of tegula; clypeus truncate in front; clypeus 3.2 × as broad as long; middle interocular distance 0.58 × the transfacial; head about 1.1 × as broad as long; lower interocular distance about equal to the upper (105); vertex very slightly arched above eyes; lateral ocelli 1.5 × as far from eyes as from each other; ratio of lengths of first four antennal joints is 50:12:60:60; pronotum almost transverse but slightly concave in center; the whole body with considerable white upright hair all over, giving a rough appearance; the ventral part of abdomen with considerable hair and last two sternites almost with a hair band; apex of all the tergites slightly rufous and last tergite yellowish white; wings yellowish hyaline with



Figs. 1 and 2.—*Priocnessus evansi*, n. sp. 1. Genitalia. 2. Subgenital plate.

Figs. 3 and 4.—*Priocnessus hurdi* Dreisbach. 3. Genitalia. 4. Subgenital plate.

veins yellow and a brown band across apical 0.7 of the second cubital cell extending backward almost to rear of third discoidal cell, apical 0.8 of wing beyond cells darkened about same amount; parameres of genitalia short and very broad; the subgenital plate, short, broad and with a characteristic darkened area sub-basally each side of midline; length head and thorax 5.3 mm, abdomen about 4.6 mm; length fore wing 9.9 mm, rear wing 7.6 mm; length genitalia 1.06 mm, width 0.93 mm; length of subgenital plate 1.26 mm, width 0.80 mm.

Type Locality.—Three miles NW. Cuernavaca, Morelos, Mex., 6500′, May 29, 1959, H. E. Evans (USNM).

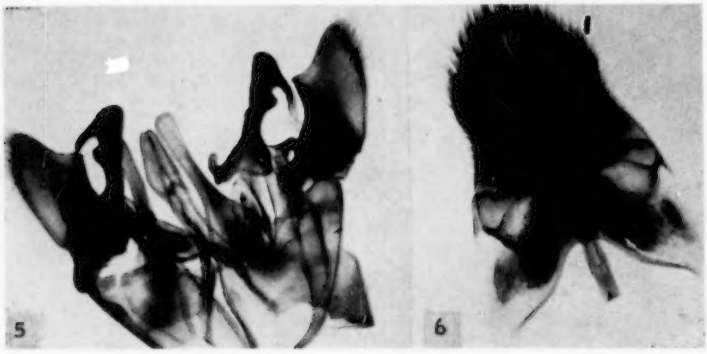
Priocnessus hurdi Dreisbach

Figs. 3 and 4

This species was described in the female sex only (Dreisbach, 1960).

Allotype Male.—Coloration almost exactly as in female except antenna is black dorsally beyond second joint, the first two joints completely rufous beneath also, but the rest of joints are brownish below; wings yellow with two faint bands as in female; subgenital plate much like *P. apache,* but basal triangle with ridges much more prominent and with two sub-basal transverse ridges at base of triangle; paramere with projection on outside near base, apicad of which is a shallow concavity and again a smaller projection; inside edge of volsellae of different shape than *apache;* length head and thorax 7.3 mm, abdomen 6.0 mm; length fore wing 11.7 mm, rear wing 9.3 mm; length genitalia 1.59 mm, width 1.3 mm; length subgenital plate 1.39 mm, width 0.86 mm.

Type Locality.—Four miles E. of Cuernavaca, Morelos, Mex., 6000′, June 7, 1956, H. A. Scullen (HAS).



Figs. 5 and 6.—*Priocnessus ruficrus*, n. sp. 5. Genitalia. 6. Subgenital plate.

Priocnessus ruficrus n. sp.

Figs. 5 and 6

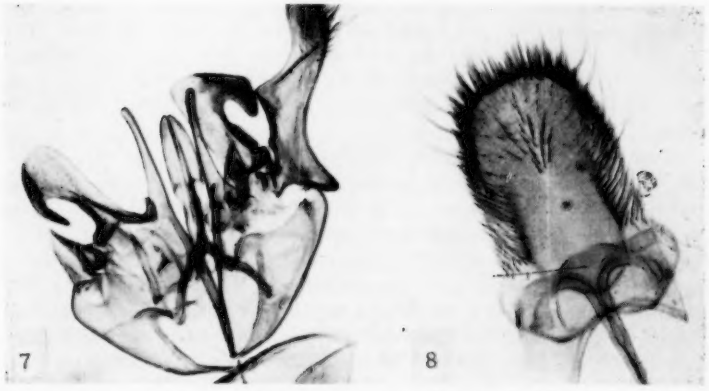
Holotype Male.—Most of front, vertex, thorax except pronotum, abdomen and coxae, black; clypeus, face, sides of front from antennae to eyes narrowing on inner orbits opposite fore ocellus, all underside of antennae, all of apical half of joint 5 through basal half of joint 8, and last tergite, yellowish white; almost all of sides of pronotum to shoulders, a band covering apical half of pronotum, tegula and base of wings, scutellum, and all femora and tibiae, rufous or with more yellowish color; apices of abdominal tergites slightly rufous and about the apical 0.25 of sixth, yellowish; fore tarsal joints rufous, the last two pair basitarsi white, the two apical joints black, the joints in between yellowish white with apex and base darkened; clypeus with a narrow irregular hairless rim, widest in middle as a short broad tooth, about 2.4 × as broad as long; head 1.15 × as wide as long; middle interocular distance a little more than 0.50 the transfacial; lower and upper interocular distance equal (95); lateral ocelli 1.5 as far from eyes as each other; ratio of lengths of first four joints of antennae is 50:15:60:55; vertex in a slight curve above eyes; posterior margin of pronotum slightly angulate; wings hyaline, shining, yellowish in reflected light, veins yellow; fourth cubital cell slightly darkened; subgenital plate broadest at base rather deeply concave about middle; parameres very broad and short, no protuberances nor concavities on outside; volsellae with a long sharp pointed hook on side subapically; length head and thorax 6.5 mm, abdomen 6.5 mm, fore wing 10.5 mm, rear wing 7.9 mm; length genitalia 1.3 mm, width 1.0 mm; subgenital plate 1.4 mm, width 0.86 mm.

Type Locality.—Four miles E. Cuernavaca, Morelos, Mex., June 16, 1956, H. E. Evans (USNM).

Priocnessus bicuspidus n. sp.

Figs. 7 and 8

Holotype Male.—Head mostly black and thorax almost entirely so, abdomen entirely rufous; face and clypeus yellowish on sides with a black longitudinal streak below and between antennae, which increases in width to apex where it occupies 0.33 of width of apex; sides of face yellowish from antennae to eyes decreasing in width on upper anterior orbits and ending in a point opposite anterior ocellus; posterior orbits same color whole length of eye; neck just behind head, the lower side of pronotum, a very narrow streak on posterior edge, and tegula, yellowish; a very short oculo-malar space black and mandible yellowish except the extreme apex is reddish; head with a few short hairs on vertex, but quite a few long yellowish hairs under head and around neck; face and clypeus with a few prostrate white hairs but not with a silvery appearance; however, the whole thorax (as well as coxae, more or less) sericeous with a rough appearance due to considerable upright hair; pronotum with hardly any dorsal surface, propodeum short, in a smooth slope; wings hyaline, slightly yellowish, evenly colored, no trace of dark clouds; veins yellow; in fore wings basal and transverse much displaced, more than length of transverse; in rear wings subdiscoidal barely apicad of cubitus; coxae black above rufous beneath; trochanters and all of rest of legs rufous; subgenital plate characterized by two small sub-basal teeth near each side, the area between them bare, the sides barely concave near base; parameres narrow for the genus, with two small protuberances on outside in basal half, with a very shallow concavity between them; volsellae with tips very short and blunt; length head and thorax 5.3 mm, abdomen 5.3 mm, fore wings 9.3 mm, rear



Figs. 7 and 8.—*Priocnessus bicuspidus,* n. sp. 7. Genitalia. 8 Subgenital plate.

wings 6.6 mm; length genitalia 1.3? mm, width 1.0? mm; subgenital plate 1.25 mm, width 0.6 mm.

Type Locality.—Four miles E. Cuernavaca, Morelos, Mex., 6000', June 29, 1959, H. E. Evans (USNM).

Paratype Males.—One same data (RRD); one same locality, date, June 20, 1959 (CU).

Priocnessus hirsutus n. sp.

Holotype Female.—Head, thorax, abdomen and legs completely black, except apex of mandible is reddish; antennae black except the joints 5-7 are yellowish white dorsally and a trace of yellowish color on underside of one or two joints at each end of the three joints; the head, thorax, and coxae very hairy, with almost shaggy black hair; femora with short hair below; abdomen hairy on last two segments; body a glossy coal black with a very faint bluish tint; the apex of clypeus with three prominent teeth, the two outside ones rather sharp, the middle one blunt, the distance between outside edge of teeth almost 0.5 × the width of clypeus at base; the edge between middle tooth and each side of outer tooth slightly concave; clypeus not raised above mouth parts as much as usual; clypeus 2.0 × as broad as long; head a little more than 1.1 × as broad as long; middle interocular distance a little more than 0.50 × the transfacial; lower interocular distance (90) equal to the upper; lateral ocelli almost 3.0 × as far from eyes as each others, ratio of lengths of first four antennal joints is 60:20:80:80; from in front vertex almost level with eyes; posterior edge of pronotum very slightly angulate; wings bright yellow with a strongly contrasting dark tip covering the outer half of membrane beyond the cells; basal vein very much basad of transverse, more than the length of the latter; in rear wings subdiscoidal and cubitus practically interstitial, the subdiscoidal vein slightly apicad; first and second recurrent veins received in the middle by second and third cubital cells; a row of about 8 teeth on inner edge of posterior tibiae with a row of small spines on outer edge set part way between them and opposite them, the shiny hairless surface between them narrowed at each tooth; length head and thorax 5.3 mm, abdomen 4.9 mm, fore wing 9.9 mm, rear wing 7.3 mm.

Type Locality.—Amecameca, Morelos, Mex., 8000', August 17, 1956, R. and K. Dreisbach (USNM).

Priocnessus nigropectus n. sp.

Holotype Female.—Most of head, all of thorax and most of abdomen black; edge of face from base of clypeus and anterior orbits to fore ocellus and a spot behind top of eye, yellowish; a small yellowish spot on each side of first tergite, a large one on each side of second tergite, and smaller spots on each side of third and fourth tergites; all coxae, trochanters, basal 0.75 of fore femora and basal 0.25 of last two pair of femora, black; rest of legs rufous except

apical one or two joints of tarsi; on last pair tarsi the extreme base of second, third and fourth joints is black; considerable long yellow hair on head, thorax and abdomen; face and clypeus and especially the thorax with a slightly golden, prostrate, glistening pubescence; clypeus with four teeth on middle of apex, the outer two slightly pointed, the middle two very broad, the space between the teeth concave; the apical part bearing the teeth only 0.5 × as wide as clypeus at base; the edge bearing the teeth hairless and polished, this area 0.3 × as long as length of clypeus; clypeus 1.35 × as broad as long; head about 1.25 × as broad as long; middle interocular distance a little more than 0.5 × as long as transfacial; lower interocular distance (95) equal to the upper; ratio of lengths of first four antennal joints is 50:18:90:80; lateral ocelli almost 3.0 × as far from eyes as from each other; antennae underneath and apex of first joint above and basal 0.6 of third joint above, rufous, remainder, brown to black; vertex straight across, same elevation as eyes; pronotum on posterior edge very slightly angled; wings yellowish hyaline, veins yellow; basal and transverse veins about as far apart as length of the transverse, and in rear wings subdiscoidal, very slightly apicad of cubitus; the first recurrent vein meets second cubital slightly beyond middle, and the second meets third cubital cell slightly beyond basal third; about 7 broad oblique teeth on inner edge of posterior tibiae, with a strong sharp spine behind them that extends about the length of teeth beyond them; an outer row of spines; the space between teeth shining, and with some long hairs; length head and thorax 6.0 mm, abdomen 6.3 mm, fore wing 10.6 mm, rear wing 7.0 mm.

Type Locality.—Mexico (ANSP).

Priocnessus tridentatus n. sp.

Holotype Female.—Head, thorax and abdomen black maculated with yellowish white; face and clypeus and inner orbits to lateral ocelli yellowish white, except for a black spot on face just below antennae continuing as a black blotch in middle of clypeus (extending about half way to apex); the color on anterior orbits broad, not pointed at apex; two yellow spots just above and continuous to antennae, and the posterior orbits with a short yellow band at base and apex of eyes; a large spot at outer lower front corners of pronotum extending backward along lower edge, continuing upward and across the posterior edge of pronotum as a wide band 0.5 × as wide as length of pronotum, irregular in front, a spot on posterior middle of mesonotum, on scutellum, postscutellum, a large spot on mesopleura just above second pair of coxae, a triangular spot under rear wing, a spot just above posterior coxae, on posterior outer corners of propodeum, a large somewhat irregular spot on each side of first four tergites (here and there with some rufous), a spot on each side of second sternite, apex of fore coxae, and part of dorsal surface of last two pairs of coxae, yellowish white; antennae rufous beneath,

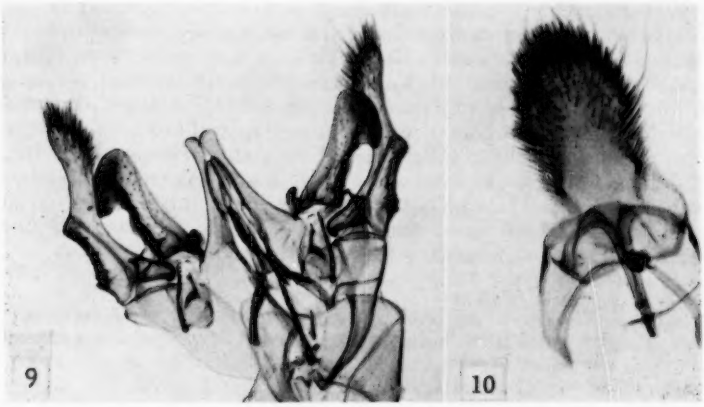
black above; coxae black except as noted, trochanters black, yellowish at apex; femora and all the rest of legs rufous, except apical tarsal joint is dark; considerable long hair over apex of abdomen, last tergite with very dark rufous hair; clypeus projects at outer front corners into large broad blunt teeth, a much smaller middle tooth, the whole apical margin inset between the two outer teeth and slightly concave on each side of middle, the very wide front margin brownish transparent; mandibles tricolored, black at base, yellow in middle, and reddish at apex; clypeus much raised above mouth parts, 2.0 × as broad as long; middle interocular distance slightly more than 0.5 × the transfacial; head 1.2 × as broad as long; lower interocular distance (160) 1.3 × the upper; lateral ocelli 2.0 × as far from eyes as from each other; ratio of lengths of first four antennal joints is 60:20:110:80; vertex level with top of eyes; posterior edge of pronotum only slightly concave in center, almost transverse; wings hyaline, yellowish, veins yellow, apical third of space beyond cells only very slightly darker; basal and transverse veins separated by more than length of transverse, and in rear wings subdiscoidal barely apicad of cubitus; first and second recurrent veins in fore wings received by second and third cubital cells at about apical 0.4 and about basal 0.4, respectively; teeth on dorsal surface of posterior tibia about like those in *P. nigropectus* but teeth are placed more nearly at a right angle to length, the teeth not so large and spines on outer edge are larger and have small teeth at their base; length of head and thorax 6.6 mm, abdomen 5.2 mm, fore wing 13.3 mm, rear wing 9.2 mm.

Type Locality.—Four miles W. of El Cercado, N. L., Mex., VI-6-1951, P. D. Hurd (PDH).

Priocnessus spinosus n. sp.

Figs. 9 and 10

Holotype Male.—Head largely black, thorax almost entirely black; abdomen rufous except for basal half of ventral and dorsal surface of first segment, and line on base of second tergite; about 0.67 of sides of clypeus, face from antennae to eyes, broad anterior orbits which narrow to an obtuse point opposite the fore ocellus, a spot behind top of eyes, upper edge of mandible, a ring almost all way around 5th and 6th antennal joints and apex of fore coxae on inside, yellowish; most of ventral surface of coxae and trochanters and all legs beyond trochanters except about the last two tarsal joints, rufous; the bases of third and fourth tarsal joints of last pair of legs, black; antennae mostly rufous ventrally beyond second joint and black on dorsal edge; face and clypeus mostly with upright yellowish hair; slightly on front and the whole thorax with golden prostrate pubescence; clypeus raised very high in middle, deeply excavated and with a small tooth in middle in front; a row of setae in middle of 5, 6 and 7th antennal joints; clypeus 2.75 × as broad as long in middle; middle interocular distance equal to 0.50 × the



Figs. 9 and 10.—*Priocnessus spinosus*, n. sp. 9. Genitalia. 10. Subgenital plate.

transfacial; head 1.14 × as broad as long; lower interocular distance (125) 1.25 × as long as the upper; lateral ocelli 1.5 × as far from eyes as from each other; ratio of lengths of first four antennal joints is 65:20:100:100; posterior edge of pronotum slightly concave in middle; wings brownish hyaline; yellowish in transmitted light; posterior trochanter with a strong blunt, short, spine on apex on inside (hence name ; subgenital plate rectangular with a broad flat slightly raised triangular (open at apex and as seen before dissection) area; a slight raised ridge near each side sub-basally, which has a small tooth at base; paramere with a large projection on outside at base and one on inside near middle; length of head and thorax 6.6 mm, abdomen 5.3? mm, fore wing 11.9 mm, rear wing 8.9 mm; length genitalia 1.7 mm, width 1.2 mm; length, subgenital plate 1.52 mm, width 0.86 mm. Mexico.

Type Locality.—San Cristobal, Casa, Chiap., Mex., 7500′, May 2, 1959, H. E. Evans (USNM).

Paratype Male.—Same data except date April 26, 1959 (RRD).

Allotype Female.—Most of head, all of thorax, extreme base of first abdominal segment, all of antennae, except apex of third and all of fourth and fifth joints, all coxae and trochanters except apex, lower basal half of mandible, and last two joints of all tarsal joints, black; about basal 0.5 of sides of thorax, face to antennae, broad anterior orbits to fore ocellus, apex of third and all of fourth and fifth antennal joints, apex of coxae, yellowish and basal half or more of mandibles, yellowish; apex and more or less underside of trochanters, all the rest of legs, except two apical joints and abdomen, rufous; clypeus black across front, grooved back of front, a flange on outer fore corners, hardly a tooth on front but the apex irregular;

clypeus about 2.3 × as broad as long; head 1.2 × as broad as long, middle interocular distance 0.56 × the transfacial; lower interocular distance 1.40 × the upper; lateral ocelli 2.0 × as far from eyes as from each other; ratio of lengths of first four antennal joints is 70:25:120:90; vertex straight across from eyes; posterior border of pronotum slightly arcuate; wings clear, but yellowish in reflected light; tegula and veins yellow except subcostal vein and vein back of it black from base to basal vein; about 7 large, narrow, flat, oblique teeth on dorsal surface of posterior tibiae, much smaller teeth on inside edge; length of head and thorax 7.3 mm, abdomen 6.0 mm, fore wing 12.2 mm, rear wing 7.9 mm. Mexico.

Type Locality.—San Cristobal I. Casa, Chiap., Mexico, April 26, 1959, 7500′, H. E. Evans (USNM).

Paratype Females.—Two. Four miles E. of Cuernavaca, Morelos, Mexico, 8000′, June 23, 1959, H. E. Evans (RRD) (CU).

Priocnessus grandis n. sp.

Holotype Female.—Body a glossy, shining black; a very faint reddish line on anterior orbits from clypeus to fore ocellus; the first five joints of antennae black the last seven yellow; the legs have a slight rufous cast about six very long hairs extending forward from front of clypeus, a great many under the mouth parts, a few on posterior orbits, above and below on fore coxae a few under fore femora, and scattered hair on the sternites; clypeus truncate in front, 2.25 × as broad as long; head about 1.1 × as broad as long; the middle interocular distance 0.5 × the transfacial distance; the lower interocular distance 1.3 × the upper; thus the eyes strongly converging above; the ocelli very large, less than their diameter part, and the lateral ones slightly nearer the eyes than to each other; ratio of lengths of first four antennal joints is 80:30:130:80; third antennal joint is 1.3 × the upper interocular distance; pronotum very short, slightly angulate on its posterior border; propodeum in a smooth curve, en-

Figs. 11 and 12.—*Priocnessus cincticornis* (Cresson). 11. Genitalia. 12. Subgenital plate.

tirely free of upright hairs; wings a dark yellowish; the basal vein basad of the transverse vein by the length of the latter; the first recurrent vein meets the first cubital cell almost at apical fourth, and the second recurrent vein meets the third cubital cell before the middle; in the rear wings the subdiscoidal vein is apicad of the cubitus by about the thickness of a vein; length of head and thorax 9.2 mm, abdomen 9.8 mm, fore wing 15.2 mm, rear wing 11.0 mm.

Type Locality.—Rio U Cayali, Peru, Dec. 2-23, F. 6178 acc. 33591, H. Bassler (Am. Mus.).

Priocnessus cincticornis (Cresson)

Figs. 11 and 12

Male.—Abdomen completely rufous except for the basal half of first tergite and basal three quarters of the first sternite; a very slight tooth on posterior trochanter; underside of first two antennal segments yellowish; a yellowish band on upper quarter of posterior orbits; subgenital plate with a short sub-basal ridge each side, subparellel and bearing outward directed hairs along its whole length; parameres rounded at apex; volsellae with a very broad hook at apex.

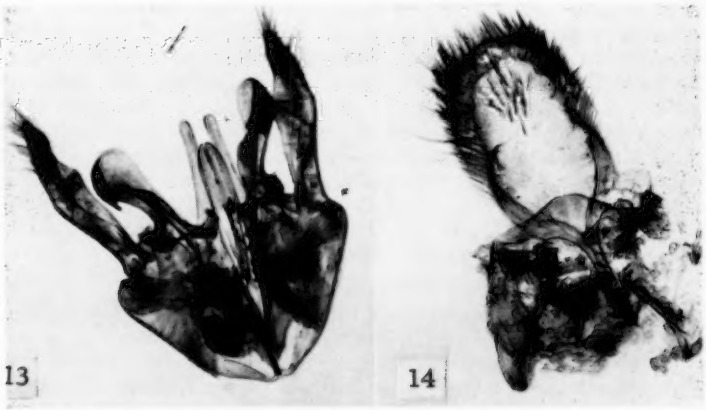
Female.—Abdomen yellowish ferruginous, except extreme bases of the first and second abdominal segments are black; the apical margins of the first and second abdominal segments and a stain on middle of second segment are fuscous; antennae black except the fourth and fifth joints are pale yellowish; apical abdominal segment is clothed with a golden pubescence. Mexico.

Priocnessus orbiculatus (Smith)

Figs. 13 and 14

Male.—Abdomen mostly black, with large yellowish spots edged with rufous on each side of the first four tergites; last tergite rufous; a plainly evident tooth at the apex on the underside of hind trochanter; underside of first antennal joint yellowish tinged with rufous; a yellowish band on the whole length of posterior orbits, except subapically; a good sized tooth in middle of apical edge of clypeus; last three joints of antennae distorted, flattened, larger than the preceding joints (do not know about this character for *P. cincticornis* as the joints beyond the fifth are lost); subgenital plate more strongly raised on basal dorsal surface, the elevation of sides bounded by a slightly curved ridge, bearing outward directed hairs only on apical half; parameres of genitalia more pointed at apex and volsellae with only a very short hook at apex. Mexico and Cuba.

Female.—Abdomen black and yellowish tinged with rufous; large yellowish spots, with rufous edges, on the sides of first three tergites; apex of abdomen rufous; sixth and seventh antennal joints white with a dark stripe; antennae yellow beneath; wings slightly darker beneath. Mexico.



Figs. 13 and 14.—*Priocnessus orbiculatus* (Smith). 13. Genitalia. 14. Subgenital plate.

REVISED KEYS TO THE NEOTROPICAL SPECIES

KEY TO FEMALES

1. White or yellow maculations on the thorax (*not* glittering spots of pubescence), head also well maculated, abdomen black with a great deal of yellow or completely rufous; wings white hyaline or slightly to strongly yellowish hyaline 2

1. No maculations on thorax but patches of silvery or golden pubescence may seem like maculations; wings generally strongly fuscous, yellowish, or reddish, in only about two species are wings yellowish hyaline 5

2. Clypeus with either one or three teeth on apical margin; abdomen black on dorsal surface (except dorsal surface of *first* tergite may be mostly yellow) maculated with yellowish spots on side 3

2. Clypeus with a small tooth on middle margin, margin each side concave; abdomen black, most of dorsal surface of first tergite yellow, two very large spots on sides of second tergite and two smaller ones on sides of third tergite, reddish yellow; first three joints antennae reddish, the rest black above, brown beneath; mandibles (except black apex) all clypeus, all face, front and broad anterior orbits to vertex, yellowish white, except a black streak in middle of front; posterior orbits all yellowish white; most of pronotum, a broad spot on mesonotum, band across scutellum, middle and posterior edge of postscutellum, a large spot above middle coxæ, smaller one under rear wing, the outer posterior corners of propodeum, and a spot above rear coxæ, yellowish white. Costa Rica..... ..... *flavidus* Dreisbach

3. Clypeus almost truncate in front; abdomen almost completely rufous on dorsal surface, base of first tergite is black and may have a yellow spot on base of first and sides of second tergite; rather broad anterior orbits, a spot on upper posterior orbits, a spot on posterior middle of *meso-*

notum, dorsal surface of scutellum, and postscutellum, yellow or yellow with some reddish 4

3. Clypeus with three teeth on apical margin; first tergite black with a yellow spot each side; a spot on each side of tergites 1-4, yellowish whole antennae black above yellowish beneath; mandibles tricolored, black at base, yellow in middle, and reddish at apex; pronotum with more black than in *flavidus*. Mexico. .....*tridentatus* n. sp.

4. Antennae with first five and a half joints and last three and one half joints black, joints in between yellow; mandibles except apex, clypeus (except black spot in middle), posterior edge of pronotum (except in middle) extending downward and covering tubercle, a large spot just above middle coxae, a large spot under rear wing, a large spot on outer posterior corners of propodeum continuing on outer corner of rim, and ventral surface of fore and middle coxae, white; fore tibiae black and white, posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior femora and tibiae, red; fore tarsi, middle tibiae and tarsi and last joint of posterior tarsi black; ventral surface of abdomen reddish suffused with black; wings almost hyaline. Brazil. ....*tricoloratus* Dreisbach

4. Antennae with first seven joints reddish (dorsal surface blackish), the rest black; mandibles (except base and apex), all of clypeus, lower side edge of pronotum, and legs beyond femora, reddish; broad posterior border of pronotum yellow with a reddish front edge; coxae, trochanters, and about basal half of femora black; abdomen with base of first tergite black and yellow and a yellow spot each side of second tergite; ventral surface of abdomen black with second and third ventrites suffused with yellow; wings with fore half of fore wing deep yellowish brown, the rear half and rear wing much lighter colored. Mexico. .....*anomalus* Dreisbach

5. Face and front densely bright golden pubescent, also some golden pubescence on thorax and abdomen 8

5. Face and front and abdomen without dense golden pubescence; thorax may have slightly golden pubescence, if so the antennae are yellow beneath and posterior orbits have a yellowish band 8

6. Face and front, densely golden pubescent, some on thorax but none on abdomen; posterior three fourths of pronotum a deep red, with silvery pubescence which appears slightly golden in reflected light; mesonotum and scutellum a deep red with no pubescence; a broad spot above middle coxae, the outer posterior corners of propodeum and the anterior corners of propodeum with brilliant shining silvery (slightly golden) appressed pubescence; the fore part of fore wing back to rear edge of second discoidal cell and covering cubital cells and fore edge of third discoidal and extending to wing tip, a deep brown, the rear of wing and all of rear wing hyaline; the contrast very prominent; exposed part of mentum and fore edge of clypeus red, the latter not much raised above mouth and concave on fore margin; abdomen red, legs black to about middle of femora then reddish; first five joints antennae reddish, last seven black. Mexico. .....*aureus* Dreisbach

6. Face, head and thorax densely covered with golden pile and prostrate pubescence; head and thorax black, but head with considerable yellowish color; coxae and trochanters black with apex yellowish; clypeus broadly yellow laterally and anterior orbits yellowish; pronotum black 7

7. Abdomen black and yellowish tinged with rufous; large yellowish spots on sides of first three tergites with rufous edges, apex of abdomen rufous; sixth and seventh antennal joints white with a dark stripe; antennae yellow underneath; wings slightly darker at tip. Mexico. ..... *orbiculatus* Smith

7. Abdomen yellowish ferruginous, except extreme base of abdomen and of the second segment black and apical margin of first and second segments and a stain on middle of second segment, fuscous; antennae black, except the fourth and fifth joints are pale yellowish; apical segment clothed with a golden pubescence. ..... *cincticornis* Cresson

8. Insect completely rufous except for sternum of thorax, tips of mandibles some sutures on thorax and base of first tergite, are black, *and* wings deep fuliginous or banded; or body completely rufous with black as above *and* wings light yellow and banded; pronotum angulate behind..... 9

8. Insect not completely rufous and wings not fuliginous or banded 11

9. Insect rufous with deeply fuliginous wings; clypeus much raised above mouth parts, an indication of a tooth in front margin and concave each side of it; first two joints of antennae reddish, last 10 joints yellowish or black underneath, black on dorsal surface; first recurrent vein received by second cubital at apical third. Mexico. ..... *rubrus* Dreisbach

9. Wings banded, with a dark band over basal veins, one over base of marginal cell and backward to rear of wing, and one on apex of wing beyond third cubital cell; wings yellowish between the bands 10

10. Insect rufous all over; only with very little black color on dorsal part of base of propodeum; no hairs on femora and no hairs on head or dorsum of thorax; head slightly longer than broad (42:40); clypeus about 2.3 × as broad as long; ratio of lengths of third and fourth antennal joints is 18:16; upper interocular distance slightly less than lower (20:22); a broad dark band over basal and transverse veins, a second one from base of marginal cell through all of second cubital and base of third cubital and across apical three fourths of third discoidal cell; clypeus hardly raised, truncate and with a slight rim; first two joints antennae reddish, rest brown beneath and black above; first recurrent vein received by second cubital cell just before middle. U.S. and Mexico..... *apache* Banks

10. Insect not rufous all over, at least ventral surface of thorax black; head broader than long; ratios of various measurements different than in *apache;* apex of propodeum as well as sutures on side of thorax black, more black on base of propodeum, black upright hair on front, vertex and dorsal surface of scutellum and postscutellum, hair on rest of body yellow; first two joints of antennae red above and below, rest of dorsal surface deep black or with the fifth and sixth joints yellow ..... *hurdi* Dreisbach

11. Body all black, at most with a slight reddish streak on anterior orbits; wings light yellow 12

11. Body not all black, either with maculations or some red color; wings generally more hyaline 18

12. Antennae, except tips, legs, and tip of abdomen fulvous; body fusco-ferruginous; wings yellowish hyaline; apex of fore wings fuscous and a cloud between the middle and apex fuscous. Cuba ..... *nubeculatus Cresson*

12. Antennae wholly black, or with basal joints to four or six yellowish and rest of antennae black; no band in fore wings 13

13. A reddish streak on anterior orbits; very hairy on head and thorax, and long hair beneath fore femora, some on mid femora above; first joint of antennae long haired; subdiscoidal vein in rear wing much apicad of cubitus; antennae black; pronotum angulate behind. Mexico. .... *rogersi* Dreisbach

13. No marks on anterior orbits or a very faint line; not quite so hairy, less hair or none on face and middle femora; no long hair on first antennal joint; subdiscoidal vein in rear wing only slightly apicad of cubitus; antennae black or partly yellow; pronotum transverse behind, or angulate in one species 14

14. A broad flange (wide tooth) in middle of front margin of clypeus; a narrow rim on clypeus; antennae black to apical fourth of third joint, yellow from there to apex of joint seven, then black to apex; thorax almost free of hair, a very few short hairs under fore femora; third antennal joint 1.2 as long as fourth; posterior tibiae with very broad teeth on inner margin of dorsal surface, very small ones on outer margin, glistening between the teeth. Mexico .....*opacus* Dreisbach

14. Without a single tooth on front margin of clypeus, either with three teeth or with none 15

15. Antennae with joints 5-7 yellow; three teeth on front of clypeus; wings bright yellow with apical 0.5 beyond cells black; pronotum angulate behind; body very hairy; mandibles reddish at apex, the only color on insect except the yellowish on antennal joints, species small in size about 10 mm in length. Mexico .....*hirsutus* n. sp.

15. Antennae wholly black, with joints 4-6 yellowish or with the last 7 joints yellow; no teeth on front of clypeus; wings hyaline, or if yellowish a darker reddish yellow and only extreme apex darkened; larger species.....16

16. Antennae wholly black or with joints 4-6 yellow; clypeus slightly concave across front, a rim on front edge of clypeus; thorax very hairy; fore and middle femora more hairy; third antennal joint 1.1 as long as fourth; although this species is larger than preceding, the teeth on inner margin of posterior tibiae only about 0.5 × as broad and opaque between teeth. Mexico .....*niger* Dreisbach

16. Antennae wholly black or the first five joints black and last seven joints yellow; thorax not hairy 17

17. Antennae wholly black, pruinose; clypeus and face below antennae densely covered with a silvery pile; clypeus elongate, obliquely narrowed toward apex, which is subtransverse; mandibles elongate, shining, apex piceous; two round spots of silvery pubescence at apex of propodeum; abdomen shining, pruinose, apical segment thickly clothed with blackish hairs, those at apex being rufous; wings hyaline, broadly violaceous at apex. Guatemala. .....*guatemalensis* Cameron

17. First five joints antennae black last seven yellow; clypeus and face without any silvery pile; no spots on silvery pubescence on propodeum; abdomen not pruinose; apical tergite with rufous hairs; wings dark yellowish with the tip only faintly blackish. Peru.....*grandis* n. sp.

18. Head and thorax with golden pubescence; head black with yellow maculations, thorax black (neck may have yellow streak) with yellow, appressed pile; abdomen ferruginous or black with yellow and reddish maculations; wings flavo-hyaline, veins yellowish 19

18. Head and thorax without golden pile, thorax and abdomen different.....22

19. Head and thorax with slight golden pubescence; head black with yellow maculations, thorax black (neck may have yellow streak) with yellow, appressed pile; abdomen ferruginous or black with yellow and reddish maculations; wings flavo-hyaline, veins yellowish 20
19. Head and thorax without golden pile, thorax and abdomen different..... 21

20. Abdomen black, maculated as follows; two preapical spots on sides of first tergite, a large spot each side in middle of second tergite, two smaller linear spots on sides of third tergite, two spots about same size on sides of fourth tergite, yellow; apices of first four tergites rufous and the last two segments entirely rufous; the first four sternites with posterior edges rufous; most of mandibles, a large spot each side of clypeus, face, broad anterior orbits, a spot in upper posterior orbits and narrow line on neck, yellow; antennae entirely black of slightly rufous near base; coxae and trochanters black; legs reddish except last joint fore tarsi, last three joints middle tarsi, and last four joints of posterior tarsi black or blackish; clypeus with a small tooth in middle, slightly concave each side, a narrow rim on apex; large teeth on posterior tibiae. Costa Rica ..... *ornamentatus Dreisbach*
20. No spots on tergites and sternites as in *ornamentatus* except apices of sternites are slightly rufous; mandibles black, except reddish apex, clypeus and face black; anterior orbits narrowly yellow and a spot on upper posterior orbits; thorax entirely black; basal 0.75 of fore femora, basal 0.5 of middle femora and basal 0.4 of posterior femora black; rest of legs rufous except apical joints of all tarsi are black; two teeth, broad and blunt, on outer edge of clypeus and two broad projections between them indicating four teeth, the edge between each two teeth slightly concave; seven narrow, oblique teeth on dorsal surface of posterior tibiae. Mexico. ..... *nigropectus* n. sp.

21. Antennae with the first two joints and base of third red, rest black; wings a strong reddish yellow, veins strongly reddish except subcosta is amber from base to slightly beyond basal vein; sides of face yellowish from base of antennae to eyes, the yellow color continuing on anterior orbits to the fore ocellus, almost as broad on front as on face; mandibles yellowish on basal half black on apical half; in certain lights, pubescence on face and thorax golden; apex of fore coxae yellow, all trochanters red; legs all red except the two apical tarsal joints; a large species 21.5 mm long. Peru. ..... *semirufus* Dreisbach
21. First two and three fourths of third antennal joints black, apex of third, the fourth, fifth and basal three fourths of six white, rest black; wings hyaline, slightly dusky, veins yellowish in reflected light; face black, anterior orbits from antennae to just before antennae with a whitish line; basal 0.75 of mandibles black, a preapical red streak, the apex black; head and thorax completely black with silvery pubescence; all coxae and trochanters black; basal half of fore femora black, and base of last two pair black, rest of legs all reddish including apical tarsal joints; a smaller species, 13.4 mm. Mexico. ..... *durangoensis* Dreisbach

22. Head, thorax and abdomen mostly black with white or yellow maculations 23
22. The whole body yellowish or at least the abdomen rufous 24

23. The sixth antennal joint entirely, the fourth broadly at apex, and the fifth at base, yellow, the rest of antennae black; mandibles (except at

apex), clypeus broadly at side, inner orbits broadly, the outer orbits more narrowly at top and bottom, the edges of pronotum all around (except in middle in front) tegula, a mark in center of mesonotum, middle of scutellum, a mark on postscutellum, two marks on mesopleura behind (the lower one the longer), a mark on lower and anterior end of metapleura, and a large mark on sides of abdominal tergites, yellow; a tooth in middle of front edge of clypeus; ventral surface obscure yellow; wings hyaline, nerves black; head and thorax opaque. Panama. .... *neotropicalis* Cameron

23. Antennae completely black; mandibles black, clypeus black; anterior orbits narrowly, a spot back of eye on temple, a small spot on anterior corners of neck, preapical posterior border of pronotum (except in center), a spot on posterior center of mesonotum, a band on scutellum, a small spot under posterior wing, a larger spot above middle coxae, a spot on outer posterior corners of propodeum, spots on extreme sides of first four tergites, yellow; legs black, but middle and posterior tibiae yellowish on posterior edge, and some on sides, these parts and tarsi with golden colored spines; a tooth on fore margin of clypeus; head and thorax (particularly thorax) shining, fore part of pronotum and neck bare and shining. Mexico. .....*octomaculatus* Dreisbach

24. Whole body pale yellowish, pronotum angulate behind 25
24. Head and thorax black or black and maculated, abdomen rufous 26

25. Antennae pale on first and second joints, black beyond; head, thorax and abdomen reddish yellow, legs and palpi also, but tarsi darker; fore wings rather yellowish in the cells, veins dark and bordered with dark or smoky, broadly so at basal vein and a broad dark cloud over most of marginal cell and back into apical part of third discoidal cell, wing tip smoky, hind wing also yellowish, tip smoky; head, thorax, coxae, venter and three apical segments with rather long fine hair; some appressed golden hair on head; both recurrent veins meet the second and third cubital cell at about middle. West Indies. .....*monticolus* Banks
25. Antennae mostly pale yellowish, but last six joints pale brown; a dark stripe above antennae each side reaching up to ocelli; a narrow black line from eye to eye; mesonotum with a broad median black mark, not reaching behind border, each side a broad black stripe from wing base forward and connected on each other behind, thus leaving a pale U in middle; scutellum with a black spot in middle of base, black behind, postscutellum yellowish across frontal part; propodeum with a large black streak each side leaving only a narrow pale median line, the dark sides narrower behind; pleura entirely pale; wings mostly hyaline, fore wings with a pale brown costal streak beyond basal vein and covering marginal, first, second, and most of third cubital cells and beyond to wing tip. Colombia. .....*bequaerti* Banks

26. Head and thorax with pale yellow or creamy white spots; clypeus, a broad streak on anterior orbits not touching clypeus, a streak on posterior orbits, an elongate spot on each side of hind margin of pronotum and the lower margin broadly and almost touching side spot of hind margin, a median spot behind on mesonotum, a small spot on scutellum, a larger one on postscutellum; one on outer side of fore coxae and several on sides of thorax, pale yellow or creamy white; petiole of abdomen and fore femora black except rufous on tip; mid and hind femora, all of tibiae, and basal part of tarsi pale yellowish, last few tarsal joints jet

black; antennae with six or six and one half joints jet black, five or four and one half creamy-white, the last joint brown; pronotum angulate behind. Trinidad. ..... *ornatus* Banks

26. Thorax not maculated and otherwise not as above 27

27. Coxae, trochanters and femora, except apex, black; apex of femora and rest of legs reddish, except last two tarsal joints of fore legs and last three tarsal joints of middle and posterior legs, black; head and particularly the thorax strongly silvery sericeous with prostrate, glistening pubescence; clypeus slightly concave in front, with a rather broad, preapical rim, which forms a slight trough (concave), particularly on the side pieces; mandibles (except tip and lower edges), sides of face, rather broad anterior orbits to lateral ocelli, and a small spot on posterior orbits just below temples, white; antennae with first two and basal three fourths of third joints black, apex of third and joints four and five, and base of six underneath, white; third joint of antennae not as long as fourth; lower interocular distance 1.3 times the upper; thorax especially shaggy, long haired, hairs light colored. Panama, Colombia. ..... *sericeus* Dreisbach

27. Legs all red except coxae and trochanters are black, and last tarsal joints are blackish; an indication of a broad tooth in middle of apical margin of clypeus and a preapical rim on clypeus; first two joints antennae black, apex of third and all of fourth and fifth bright yellow, rest of antennae black 28

28. Sides of clypeus at base, fairly wide anterior orbits from clypeus to lateral ocelli, a linear spot on posterior orbits just below temples, most of mandibles and all mentum, *reddish; pronotum deep red;* wings light yellow; teeth on posterior tibiae very small; length about 14.5 mm long. Ecuador. ..... *caesius* Dreisbach

28. Sides of clypeus at base of about 0.75 of width, yellowish, the color narrowing toward apex so that at about middle of clypeus it covers about 0.4 of width, about 0.3 of apex black; face below antennae and a mark in middle of sides at base of clypeus black the rest yellow and the color continuing on anterior orbits broadly, to beyond fore ocellus; mentum black, and all of abdomen black; mandibles yellow on basal 0.5, dark on apical 0.5; large teeth on inner edge of dorsal surface of posterior tibiae, and fairly good sized teeth on outer edge, long scattered hairs between the teeth; length about 13.0 mm. Mexico. ..... *spinosus* n. sp.

KEY TO MALES

1. Clypeus entirely yellow or mostly yellow with a dark spot or band in middle 2

1. Clypeus with no yellow marks whatever; very narrow yellowish mark on anterior orbits in one case 10

2. Last trochanter with a strong tooth on apex of under side *and* abdomen red, legs red (including underside of coxae) except last two or three tarsal joints which are black; first two joints of antennae red, the rest black; head and thorax with golden prostrate pubescence spotted over most of surface; wings rather strongly fumous, yellowish; subgenital plate somewhat elevated, rectangular, with spines over apical sides and across apex; clypeus yellow with a large black spot in middle; mid and posterior tarsi black beyond basal joint. Peru and Colombia..... *prominens* Banks

2. If a strong tooth on apex of hind trochanter, a black band lengthwise in middle of clypeus 3

3. Clypeus completely white 4
3. Clypeus white at sides, a longitudinal black band in middle 7

4. Wings hyaline without bands, only apex of wing darker; face entirely yellowish as well as most of pronotum; apical tergite whitish and apex of preceding tergite rufous; abdomen black; subgenital plate with base wider than apex and strongly restricted in width *above* middle of plate, dark colored; parameres very broad, short and with no protuberances on outsides. Mexico. ..... *ruficrus* n. sp.
4. Wings with bands and hyaline between bands or the wings strongly darkened, so bands are not so evident; subgenital plate different 5

5. Wings very much darkened but with slightly stronger color over basal veins and cubital cells; thorax mostly rufous; coxae, trochanters and first two antennal joints rufous as well as abdomen; no protuberances on outside of trochanters near base; all femora rufous; size large 13.5 mm. Mexico. ..... *hurdi* Dreisbach
5. Wings banded over basal veins (or not) and cubital cells, hyaline (brownish) between bands; apex of wing dark; coxae and trochanters black 6

6. Abdomen black, first two joints of antennae black above; thorax black; all femora rufous; no cloud over basal veins; subgenital plate more nearly rectangular with a sub-basal dark cloud each side near middle; parameres much broader and slightly concave on outside at base. Mexico. ..... *evansi* n. sp.
6. Abdomen rufous; first two joints of antennae completely rufous; posterior femora mostly black; a cloud over basal veins; pronotum rufous and rest of thorax with some rufous; subgenital plate more ovoid not rectangular, with no dark cloud; parameres much narrower, straight on outside. U.S. and Mexico. ..... *apache* Banks

7. Thorax and sometimes the head with golden pubescence; a small or a strong tooth on underside of hind trochanter at its tip; no prominent tooth sub-basally near the sides on subgenital plate, this is plainly visible without dissection; neck and pronotum black 8
7. Neither head nor thorax with golden pubescence, but pubescence is silvery but slightly yellowish in certain light; no trace of a tooth on posterior trochanter; a prominent tooth sub-basally near sides on ventral surface of subgenital plate near the sides, visible without dissection; neck with a white spot where it joins the head, and the lower side of pronotum yellowish. Mexico. ..... *bicuspidatus* n. sp.

8. A strong thick obtuse tooth on apex of ventral side of hind trochanter; abdomen rufous, except basal half of first segment; golden pubescence strong on thorax; legs all rufous beyond trochanters except apical tarsal joints; a larger species. Mexico. ..... *spinosus* n. sp.
8. Either a small tooth or barely an indication of one; golden pubescence not so strong on thorax 9

9. Abdomen completely rufous except for about the basal 0.5 of first tergite and basal 0.75 of first sternite; a very slight tooth on posterior trochanter; underside of first two antennal joints yellowish; a yellowish

band on upper 0.25 of posterior orbits; subgenital plate with a short sub-basal ridge each side, subparallel and bearing outward directed hairs its whole length; parameres and volsellae rounded at apex. Mexico. ..... *cincticornis* (Cresson)

9. Abdomen mostly black, with large yellowish spots edged with rufous on each side of the first four tergites, last tergite rufous; a plainly evident tooth at apex on the underside of last trochanter; underside of first antennal joint yellowish tinged with rufous; a yellowish band on the whole length of posterior orbits, except subapically; a good sized tooth in middle of apical edge of clypeus; last three joints of antennae distorted, flattened, larger than preceding joints (do not know about *cincticornis* as joints beyond the fifth are last); subgenital plate more strongly raised on basal dorsal surface, the sides of elevation bounded by a slightly curved ridge, bearing outward directed hairs only on apical half; parameres more pointed on apex and volsellae truncate across apex, slightly emarginate. Mexico and Cuba. ..... *orbiculatus* (Smith)

10. Narrow yellow lines on anterior orbits from base of clypeus or just above; clypeus with three teeth on front margin, middle one small triangular, the sides concave each side to the lateral broader teeth; clypeus much raised above mouth parts, strongly arched. 11

10. No marking on anterior orbits, body wholly black; clypeus *without* teeth, concave on front margin or almost truncate. 13

11. Antennae wholly black; wings reddish with contrasting black tip; subgenital plate elongate, gradually narrowing from base to broad obtuse apex; a few long hairs almost as long as width of plate on sides near apex and around apex; a raised hairless area, broad at base then gradually converging to apical fourth, sides above base subparallel; parameres of genitalia with a large concavity on outside near base. Mexico. ..... *lineatus* Dreisbach

11. Antennae with some joints completely yellow; wings reddish with a black cloud in second cubital and third discoidal cell, or hyaline with black veins; subgenital plate shorter and ovate, or as long but sides concave just above base. 12

12. Antennal joints 5-8 completely yellow, joints 3, 4 and 9-11 yellow beneath, black on dorsal surface; linear impressions on joints 6-8; wings reddish yellow with a blackish cloud in second cubital and third discoidal cell; apex of wing blacker than in *lineatus* covering most of third discoidal cell; subgenital plate much shorter than in *lineatus*, ovate, triangular area shorter, not as broad; shorter hair on sides and around apex; parameres of genitalia short and broad, the outside edge straight without a large concavity. Mexico. ..... *kayi* Dreisbach

12. Some of middle antennal joints yellow; wings hyaline with dark veins; subgenital elongate, with the sides just above base concave, a broad basal triangle which is open at apex, the prominent sides of triangle ending about middle of plate; parameres of genitalia much more slender and longer than in *kayi*. *Panama*. ..... *neotropicalis* (Cameron)

13. Head and thorax with hair black, only slightly reddish in reflected light, no appressed reddish pubescence; clypeus hardly raised above mouth parts and truncate in front; eyes reach vertex; pronotum transverse behind; subdiscoidal vein of rear wing is interstitial with the cubitus; no teeth and only a very few small spines on posterior tibiae; subgenital

plate concave on sides about middle, the upper half of plate semiorbicular, the raised portion at base wider than in next; size smaller about 13 mm long. Honduras. .....*hondurensis* Dreisbach

13. Head and thorax with reddish black hair and with appressed reddish pubescence; clypeus raised above mouth parts and concave on front margin; pronotum angulate behind; subdiscoidal vein in rear wings apicad of cubitus; small teeth and spines on dorsal surface of posterior tibiae; subgenital plate almost rectangular, only slightly concave on sides near middle, the upper half with sides parallel to close to apex; size larger about 15 mm. Mexico. .....*rogersi* Dreisbach

REFERENCES

CRESSON, E. T. 1867. Notes on the Pompilidae of North America with descriptions of new species. *Trans. Am. Entomol. Soc.*, **1**:120.

DREISBACH, R. R. 1960. Seventeen new species in the genus Priocnessus (Hymenoptera: Psammochariae) with keys to males and females of all known Neotropical species. *Am. Midl. Nat.*, **63**(2):335-364.

Three New Species of the Genus Entocythere (Ostracoda, Cytheridae) from North and South Carolina[1]

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ABSTRACT: Investigations on the ostracods epizoic on crayfishes has led to the discovery of three new species. A morphological treatment along with taxonomic consideration is accorded each of these new forms. The known range of each new species together with the host relationships is presented.

In studying commensal ostracods of the genus *Entocythere* Marshall (1903) of western North Carolina and northern South Carolina, three new species were encountered and are described herein. One of them is a member of the Columbia Group Rioja (1949) and the other two are distinctly related to members of the Runki Group Crawford (1959).

Insofar as is known, the members of this genus are all associated with crayfishes, and the determinations of the hosts of the three new species were made by Dr. Horton H. Hobbs, Jr. of the University of Virginia. These crayfishes have been deposited in his personal collection.

The methods utilized in this study were similar to those outlined by Crawford (1959:149).

Entocythere clemsonella[2], sp. nov.

Male.—Valve (Fig. 7) suboval in lateral aspect with the anterior and ventral margins smoothly rounded. Dorsal margin slightly arched along posterodorsal edge. Setae sparsely scattered on lateral surface of valve and irregularly dispersed along free margin. Eye located about one-sixth of valve length from anterior end. Valve size relatively constant as indicated by the measurements of 10 specimens from the type locality mounted in Hoyer's solution: length, 0.345 mm to 0.375 mm, average, 0.361 mm; height, 0.210 mm to 0.225 mm, average, 0.214 mm.

Antenna I with six podomeres, the basal one is longest and third from base shortest; three distal podomeres subequal in length. Diam-

[1] This study was made possible by a grant from the American Association for the Advancement of Science through the South Carolina Academy of Science.

[2] This species is named in honor of the late Thomas Green Clemson, distinguished diplomat, able mining engineer, active promoter of scientific education in the United States, and founder of Clemson A & M College.

eters of successive podomeres diminish regularly distally. One seta borne on apical end of both first and second podomeres with two on third. Antepenultimate podomere with six setae, penultimate devoid of setae, and ultimate with five terminal setae.

Antenna II (Fig. 1) with four podomeres; basal one bearing subapical antennal flagellum. Antepenultimate podomere little wider than long, with distal flexor margin bearing a heavy, feathered, spine-like seta. Penultimate podomere with two setae borne on apical flexor margin. Ultimate podomere apparently divided toward apical end and with heavy setae in notch on midflexor margin. Characteristic terminal claws borne on distal portion of ultimate podomere; dorsal claw stalked and prominently arched proximally with flattened distal surface bearing 10-12 teeth; middle claw short and toothed, and ventral claw arched distally with cluster of teeth on ventrodistal surface.

Mandible (Fig. 2) with protopodite bearing a row of six multicuspid teeth distally; the two proximal teeth with one or two cusps, the middle three with three cusps, and the distal tooth with five. Heavy seta borne in notch on convex surface of protopodite at level slightly proximal to proximal tooth. Respiratory plate with three setae. Palp consisting of four indistinct podomeres; basal one with long seta borne on distal flexor margin; short antepenultimate podomere without setae; penultimate podomere with two setae, one of which is borne in notch on midextensor margin, the other arising from apical end; and short ultimate podomere with three heavy setae on distal end.

Maxilla (Fig. 4) with protopodite bearing two terminal setae. Unsegmented palp with two apical setae, the ventral one being heavier. Conspicuous notch present on dorsal surface of palp. Respiratory plate with 15-20 plumose setae.

Copulatory complex (Fig. 5). The proximal portion of the base is subspatulate in shape, somewhat similar to that of *E. telmoecea* Crawford (1959). Attached to the proximal portion of the base are the dorsal and ventral fingers; the latter is more attenuated and longer than the former; the terminal spine of the former appears to be bifurcate. The distal portion of the base is long and narrow, the posterior margin bearing a concavity at its midlength. The anterior and posterior margins join to form an acute angle. The rami of the clasping apparatus (Fig. 3) form an angle of about 70 degrees. The flexor surface of the horizontal ramus bears three teeth on the distal half which decrease in prominence distally. The entire extensor margin of the horizontal ramus is smooth. Four prominent teeth are borne on the distal end of the horizontal ramus.

Female. The valve of the triunguis forms (Fig. 6) is suboval in lateral aspect with the ventral margin bearing a slight concavity just anterior to midlength. The dorsal and anterior margins are evenly rounded with the posterior one being slightly arched. The free margins of the valve are setiferous, and the lateral surface sparsely so. The

eye is located one-fifth of valve length from the anterior end. The measurement of 10 specimens from the type locality mounted in Hoyer's solution exhibit a range in length of 0.395 mm to 0.420 mm, with an average of 0.410 mm; in height the range is 0.240 mm to 0.270 mm, and averages 0.258 mm.

The second antenna of the triunguis female generally bears three terminal claws; however some specimens apparently have only two. The dorsal claw, bearing a few teeth on the distal end, is about two-thirds as long and more slender than the ventral claw. The very slender middle claw is two-thirds as long as the dorsal claw, and is without teeth on the distal end. The ventral claw is heavy and has 10-15 teeth on the ventrodistal surface.

The valve of the biunguis female (Fig. 8), in lateral aspect, is oval, being slightly arched along the posterodorsal margin. It is slightly smaller than that of the triunguis form.

The genitalia of the triunguis female consists of a short, thick, heavily sclerotized, hollow tube (*pieza quitinosa femenina*), Rioja (1943:575) which is directed ventrad.

Type Locality.—Small, intermittent stream on S. C. Route 20 about 1.4 miles north of Abbeville, Abbeville County, South Carolina. The crayfish host here is *Cambarus latimanus* LeConte (1855). *E. internotalus* Crawford (1959) and *E. striophylax* Crawford (1959) were also found in collections from the type locality.

Disposition of Types.—The holotypic male, the allotypic (triunguis) female, the morphotypic (biunguis) female, and a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

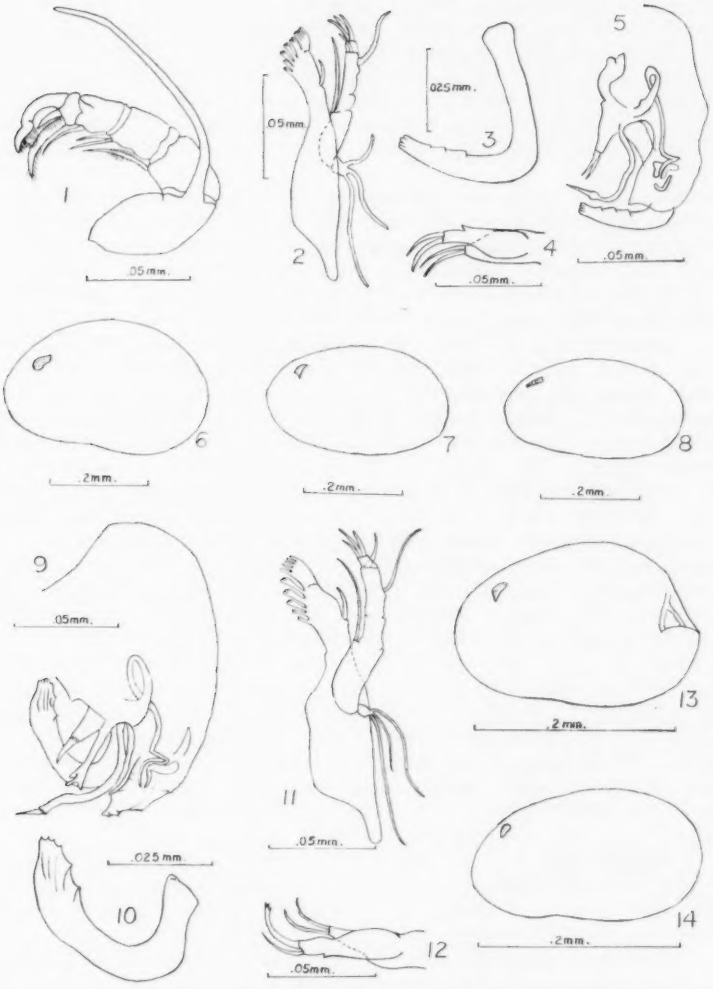
Range.—This species was found in two collections other than that from the type locality: (1) a tributary of Little River in Rock Eagle Park, Putnam County, Georgia, and (2) Skeleton Creek near Gaffney, Cherokee County, South Carolina.

Remarks.—This species seems to be closely related to *E. riojai* Hoff (1943) and *E. equicurva* Hoff (1944). There is a striking similarity in the clasping apparatus of this species to that of *E. riojai* although the proportionate lengths of the vertical and horizontal rami readily separate the two species; the vertical ramus is relatively longer in the latter. The character of the horizontal ramus of this species easily distinguishes it from that of *E. equicurva*. The C-shaped clasping apparatus definitely places *E. clemsonella* in the Columbia Group Rioja (1949).

Entocythere leptophylax[3], sp. nov.

Male.—Valve (Fig. 14) subelliptical with anterior end narrower than posterior. Margins smoothly rounded except for slight concavity

[3] This name is derived from Greek (leptos — narrow; phylax — guard) and refers to the narrow, thin, finger guard.



Figs. 1-8.—*Entocythere clemsonella* sp. nov. 1. Antenna II of male. 2. Mandible of male. 3. Clasping apparatus of male. 4. Maxilla of male. 5. Copulatory complex of male. 6. Lateral aspect of valve of triunguis female. 7. Lateral aspect of valve of male. 8. Lateral aspect of valve of biunguis female. Figs. 9-14.—*Entocythere leptophylax* sp. nov. 9. Copulatory complex of male. 10. Clasping apparatus of male. 11. Mandible of male. 12. Maxilla of male. 13. Lateral aspect of valve of triunguis female. 14. Lateral aspect of valve of male.

on ventral margin just anterior to midlength. Height greatest slightly posterior to midlength. Setae scattered along free margin of valve but more numerous on anterior end; lateral surface with few widely spaced setae. Eye located about one-sixth of valve length from anterior end. Valve size of ten specimens from type locality mounted in Hoyer's solution indicates a range in length from 0.435 mm to 0.465 mm, average, 0.450 mm; height, 0.240 mm to 0.290 mm, average, 0.273 mm.

Antenna I with six podomeres; the basal one is longest with second, third, and fourth subequal in length. Ultimate podomere about two-thirds as long as basal one. One seta borne on distal ends of first and second podomeres with two in corresponding position on third. Antepenultimate podomere with six long setae, penultimate devoid of setae, and ultimate with five terminal setae.

Antenna II with four podomeres; basal one devoid of setae but with a long, thin, antennal flagellum on apical end. Second podomere with feathered, spine-like seta on distal flexor margin. Penultimate podomere with two setae on distal flexor extremity. Ultimate podomere divided toward apical end; proximal portion bearing a seta on distal flexor margin. Distal portion of ultimate podomere with the three characteristic terminal claws: stalked dorsal claw arched proximally with flattened distal surface distinctly toothed; short, toothed, middle claw stalked; and ventral claw, the longest, bearing numerous teeth on distal portion of ventral margin.

Mandible (Fig. 11) with a row of six or seven multicuspid teeth borne on distal end of protopodite; proximal tooth bicuspid, middle three tricuspid, and prominent distal tooth with five cusps. Convex surface of protopodite with heavy seta at level of proximal tooth. Respiratory plate with three setae, two relatively long and subequal in length, and one about one-half as long as others. Mandibular palp with four indistinct podomeres; basal one with long seta borne on distal flexor margin; antepenultimate podomere devoid of setae; penultimate podomere with a single long seta arising from prominent notch on mid-extensor surface and with a short seta on apical end; ultimate podomere short and with three terminal setae.

Maxilla (Fig. 12) with unsegmented palp bearing two setae on apical end, the ventral one longer, heavier, and denticulate distally. Extensor surface of palp with prominent notch. Protopodite with two long, thin, terminal setae.

Copulatory Complex (Fig. 9). The proximal and distal portions of the base are not clearly distinguishable. Attached to the former are the short dorsal and long ventral fingers; the latter is more attenuate and is distinctly stalked subdistally. Both dorsal and ventral fingers terminate with the characteristic spine. The heavily sclerotized finger guard is conspicuously narrow and long, with the distal end prominently trilobed. The distal portion of the base is wide dorsally tapering to an acute point ventrally. The posteroventral margin is sclerotized with two small tooth-like projections at the ventral ex-

tremity. The horizontal and vertical rami of the clasping apparatus (Fig. 10) are not clearly delimited, and do not occupy the descriptive positions; for this reason they are here referred to as the proximal and distal rami. The former is approximately one-half as long as the latter and the angle formed by the two is about 60 degrees. The distal ramus is enlarged distally with six or more subapical serrations of which the two proximal ones are most prominent.

Female.—The valve of the triunguis forms (Fig. 13) is higher posteriorly than that of the male, and the ventral margin has a slight concavity just anterior to midlength. The dorsal margin is prominently arched, the anterior one smoothly rounded, and the posterodorsal margin concave. The measurements of ten specimens from the type locality mounted in Hoyer's solution exhibit a range in length of 0.465 to 0.510 mm, averaging 0.491 mm. The range in height is 0.300 mm to 0.330 mm, with an average of 0.312 mm.

The second antenna of the triunguis female has two or three terminal claws, of which the ventral one is thicker, longer, and heavier toothed. The unstalked dorsal claw is about three-fourths as long as the heavier ventral claw, and bears a few teeth on the distal end. The inconspicuous middle claw is without teeth and is two-thirds as long as dorsal claw.

The genitalia of the triungius female (Fig. 13) are subtriangular and show considerable variation. Unlike other members of this group, the triunguis female is without the deeply staining mass associated with the genitalia.

No description can be made of the biunguis female as no copulating forms were observed.

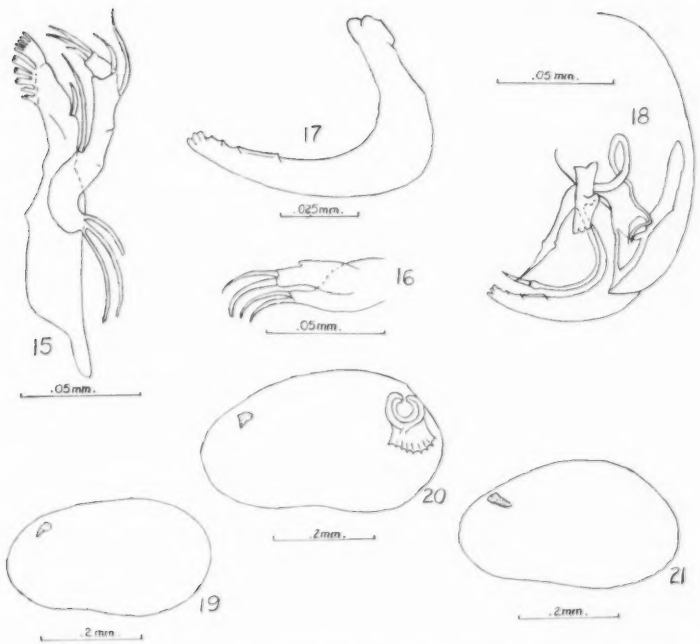
Type Locality.—East Fork of the Chattooga River at its junction with Indian Camp Creek on the grounds of the U.S. Fisheries Station, 21 miles northwest of Walhalla, Oconee County, South Carolina. The hosts are *Cambarus asperimanus* and *Cambarus bartoni bartoni.* Two other ostracods, *E. humesi* Hoff (1943) and an undescribed species were collected from the type locality.

Disposition of Types.—The holotype, the allotypic (triunguis) female, together with a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

Range.—This species is known only from the type locality.

Variations.—There is remarkable uniformity in the male copulatory complex except that the finger guard is slightly wider in some specimens than in others. There are slight variations in the valve shape of both male and female.

Remarks.—E. leptophylax, without question, is to be placed in the Runki Group Crawford (1959) by virtue of the possession of the finger guard, an accessory process of the copulatory complex. The intragroup affinities of this species are highly uncertain as there appears to be a marked contrast between the copulatory complex of



Figs. 15-21.—*Entocythere chelomata* sp. nov. 15. Mandible of male. 16. Maxilla of male. 17. Clasping apparatus of male. 18. Copulatory complex of male. 19. Lateral aspect of valve of biunguis female. 20. Lateral aspect of valve of triunguis female. 21. Lateral aspect of valve of male.

E. leptophylax and those of the other four species of this group. The expanded apical end of the distal ramus of the clasping apparatus is similar to that of *E. humsi* Hoff (1943).

Entocythere chelomata[4], sp. nov.

Male.—Valve (Fig. 21) oval in lateral aspect with margins smoothly rounded. Posterior end higher than anterior with maximum height just posterior to midlength. Prominent eye located one-fifth of valve length from anterior end. Setae sparsely distributed on lateral surface and dispersed as usual along free margin. Valve size is relatively constant as indicated by measurements of ten specimens from the type locality mounted in Hoyer's solution: length 0.420 mm to

[4] Cheloma G. a notch; so named because of the notch on the finger guard of the clasping apparatus of the male.

0.465 mm, average 0.448 mm; height 0.250 mm to 0.270 mm, average 0.264 mm.

Antenna I similar to that of *E. leptophylax* described above.

Antenna II composed of four podomeres of which the basal one bears the antennal flagellum on apical end. Second podomere with feathered, spine-like seta borne on distal flexor margin. Penultimate podomere with two setae on apical flexor margin. Ultimate podomere divided distally with spine-like seta on midflexor margin of proximal portion, and bearing distally three terminal claws: dorsal one stalked with flattened, toothed distal surface; middle claw short with ten or more long teeth along ventral margin; and ventral claw longest and arched distally with a row of conspicuous teeth on ventrodistal surface.

Mandible (Fig. 15) with protopodite bearing six or seven multicuspid teeth; proximal two bicuspid, the next three tricuspid, and the distal tooth with five cusps. Heavy, spine-like seta borne on convex surface of protopodite proximal to proximal tooth. Respiratory plate with three setae, two subequal in length, and the third one half as long as the others. Palp consisting of four indistinct podomeres; except for the antepenultimate, each podomere with one or more setae.

Maxilla (Fig. 16) with protopodite bearing two long, thin setae distally and respiratory plate with about 20 plumose setae proximally. Unsegmented palp with two apical setae; the ventral one heaviest and apparently expanded distally. Convex surface of palp with slight notch opposite level of apical end of protopodite.

Copulatory Complex (Fig. 18). Attached to the indistinctly delimited proximal portion of the base are the short dorsal and long ventral fingers with spinous apices. The heavily sclerotized finger guard appears to be partially divided transversely at midlength, and the distal portion is broader than the proximal and trilobed apically. The posterior margin of the distal portion of the base is smoothly rounded terminating distally in an acute angle. The vertical ramus of the clasping apparatus (Fig. 17) is distinctly arched, is clavate proximately, and bears a prominence on the posterior margin. The longer horizontal ramus is slightly arched and bears four serrations on the distal half of the flexor margin and three prominent teeth on the apical end.

Female.—The valve (Fig. 20) of the triunguis forms is subovate with concavities on the posterodorsal and ventral margins, the latter being slightly anterior to midlength. The pubescence is similar to that on the valve of the male. The size is relatively constant as indicated by the measurement of 10 specimens from the type locality mounted in Hoyer's solution show a range in length of 0.435 mm to 0.480 mm, averaging 0.456 mm. The range in height is 0.255 mm to 0.300 mm, with an average of 0.278 mm.

The second antenna of the triunguis females has two or three

terminal claws, the ventral one being longer, heavier, and more prominently toothed than the smaller dorsal claw. The dorsal claw is three-fourths as long as ventral one and with few, if any, inconspicuous teeth. The untoothed middle claw, when present, is very narrow and about three-fourths as long as the dorsal claw.

The unique genitalia of the triunguis female (Fig. 20) consist of a pair of conspicuous circular, O-shaped, rod-like structures ventral to which is a prominent "pleated skirt."

The valve of the biunguis female (Fig. 19) is similar to that of the triunguis female except that it is smaller and is lacking the posterodorsal concavity.

Type Locality.—West Fork of the Little Pigeon River, one mile south of Gatlinburg, Sevier County, Tennessee, on U. S. Highway 441, in the Great Smoky Mountain National Park. The hosts are *Cambarus longulus longirostris*, *Cambarus bartoni bartoni* and *Orconectes juvenilis*. Three other ostracods, *E. humesi* Hoff (1943), *E. daphnioides* Hobbs (1955), and an undetermined member of the Cambaria Group, were collected from the type locality.

Disposition of Types.—The holotype, the allotypic (triunguis) female, and the morphotypic (biunguis) female along with a dissected male paratype are deposited in the United States National Museum. Paratypes are in the collections of Drs. Horton H. Hobbs, Jr., Eugene N. Kozloff, and the author.

Range.—Besides the type locality, this species is known to inhabit the Sugar Fork (Cullasaga) River northwest of Highlands, Macon County, and the Valley River at Andrews, Cherokee County, North Carolina. In the Sugar Fork River the host was *Cambarus bartoni bartoni* and in the Valley River the hosts were *Cambarus bartoni bartoni* and *Cambarus longulus longirostris*.

Variations.—Slight differences occur in the degree of concavities on the anteroventral and posterodorsal margins of the shell. The circular, O-shaped, rod-like bodies of the triunguis female genitalia were noted to assume a U-shaped appearance in some specimens, and were found to protrude beyond the posterodorsal margin of the valve in a considerable number of them.

Remarks.—The closest relatives of this species seem to be *E. runki* Hobbs (1955) and *E. suteri* Crawford (1959), differing from the former in the slenderness of the horizontal ramus of the clasping apparatus, and the more proximal serrations on the finger margin of *E. runki* are much more prominent and evenly spaced than are those of *E. chelomata*. The over-all outline of the clasping apparatus of *E. suteri* is similar to *E. chelomata*. The proximal end of the vertical ramus of the clasping apparatus of *E. suteri* appears to be evenly rounded while that of *E. chelomata* is conspicuously knobbed. One of the outstanding features of this species is the unique genitalia of the triunguis female. The finger guard of *E. chelomata*, which places it in the Runki Group Crawford (1959), bears a distinct notch at midlength while those of *E. runki* and *E. suteri* are entire.

REFERENCES

CRAWFORD, E. A., JR. 1959. Five new ostracods of the genus *Entocythere* (Ostracoda, Cytheridae) from South Carolina. *Univ. So. Car. Pub. Biol., Ser.* III, **2**(4):149-189.

HOBBS, H. H., JR. 1955. Ostracods of the genus *Entocythere* from the New River system in North Carolina, Virginia, and West Virginia. *Trans. Am. Microscop. Soc.*, **74**:325-333.

HOFF, C. C. 1943. Two new ostracods of the genus *Entocythere* and records of previously described species. *J. Wash. Acad. Sci.*, **33**:276-286.

———1944. New American species of the ostracod genus *Entocythere*. *Am. Midl. Nat.*, **32**:327-357.

MARSHALL, W. S. 1903. *Entocythere cambaria* (nov. gen. et. nov. sp.), a parasitic ostracod. *Trans. Wisc. Acad. Sci.*, **14**:117-144.

RIOJA, ENRIQUE 1943. Estudios Carcinologicos. XV. Polimorfismo Femenino en los Ostracodos del genero *Entocythere*. *An. Inst. Biol. Mex.*, **14**:567-585.

———1949. Estudios Carcinologicos. XXI. Contribucion al Conocimiento de las Especies del Genero *Entocythere* de Mexico. *An. Inst. Biol. Mex.*, **20**:315-329.

Notes and Discussion

Spore to Spore Culture on Agar of Stemonitis fusca

Alexopoulos (Am. J. Bot. 46:140-142. 1959) reported for the first time the cultivation on laboratory media of a member of the Stemonitales, *Stemonitis flavogenita*. He was later (Am. J. Bot. 47:37-43. 1960) able to carry through its life cycle another species at present included in the same order, *Echinostelium minutum*. With the exception of these two species, members of the order Stemonitales have not been cultured on laboratory media, to the writers' knowledge. This communication reports the cultivation of a third member of the Stemonitales, *Stemonitis fusca* Roth.

Spores from sporangia which had fruited on bark in a moist chamber in the laboratory were transferred to 1.5 per cent Difco corn meal agar plates on October 3, 1959. Small plasmodia had developed in most of the plates in seven days, and large veins with active streaming were present two weeks after inoculation. The cultures were maintained at room temperature in the dark and given water and dry cereals at intervals. By January 15, 1960 the plates contained abundant plasmodia. In an effort to induce fruiting, some of the plates were placed in direct sunlight for three hours and in daylight thereafter. Within three days they had fruited.

The organism has been kept continuously in culture since that time, and spores from the third generation grown on agar have now produced plasmodia. A study of the method of plasmodium formation, the fruiting process, and other phases of the life cycle is in progress.

The plasmodium of *Stemonitis fusca* corresponds closely with that of *S. flavogenita* as described by Alexopoulos. The plasmodium is delicate and almost transparent until fruiting is about to occur; at that time it becomes white and opaque. It has never been observed to turn yellow in our cultures. The long main veins with very short secondary branches are the outstanding characteristic of the well-developed plasmodium, in contrast to the fan of the Physarales. At the forwardmost portion of the moving or feeding plasmodium, however, anastomoses becomes more frequent, so that in this area the morphology of the physaraceous fan is approached. The high incidence of vacuoles as described for *Stemonitis flavogenita* was noted also in our material.

Our thanks to Professor G. W. Martin and Professor C. J. Alexopoulos for verifying our determination of the *Stemonitis* species.—Sister M. Annunciata McManus and Sister M. Vianney Richmond, Mount Mercy College, Cedar Rapids, Iowa.

Book Reviews

IN AND OUT OF THE IVORY TOWER. The Autobiography of Richard B. Goldschmidt. University of Washington Press, Seattle. xiii + 352 p., 27 figs. 1960. $5.75.

Richard B. Goldschmidt died on April 24, 1958, just twelve days after his eightieth birthday and less than a week after completion of this manuscript. We are indebted to Dr. Curt Stern and to Dr. Leonie K. Piternick for the arduous task of seeing it through to publication.

This book is complementary to "Portraits from Memory," in which Goldschmidt presented his recollections of the great German zoologists of the late eighteenth and early nineteenth centuries. Many of the same people — Bütschlli, Boveri, R. Hertwig, and so many others—appear in both books. In the Portraits, however, these men are the central figures, Goldschmidt only the narrator. The present book is his own story, and the others appear as his teachers, collaborators, and colleagues. All of these men met and worked together in the Ivory Tower of the academic community, but they took long excursions "out," and we see Goldschmidt not only as the man who developed the Kaiser Wilhelm Institute for Genetics, but also as a world traveller, an enthusiastic collector of art, a *bon vivant*, a mountain climber and hiker, and a devoted husband and father.

Because the emphasis is placed outside the Ivory Tower and because the glimpses within avoid technical aspects of his work, this book will be as comprehensible and fascinating to the educated public as to biologists. In the first chapters, there is given an insight into education in late imperial Germany which, to this reviewer, was as absorbing as it was informative.

Three times Goldschmidt visited Japan and other Oriental countries, and he also travelled widely elsewhere. The story of these travels is told with an excellent selection of interesting incidents and sympathetic and discerning description of the local cultures.

The tragedy of two World Wars looms large in this story. Goldschmidt was "caught" in the U.S. when World War I broke out. A patriotic German, he wanted to return and serve in the army. This was not possible, but he did succeed in bringing his family to the U.S. Although he had research facilities at Yale, he and his family were exposed to bitter enmity simply because they were Germans. After the U.S. entered the war, he was interned as an enemy alien. Even during this humiliation, he played the violin in a symphony orchestra, taught a course in biology in the camp "university," studied Spanish and Chinese, and wrote a book which was later very successful and was translated into several languages.

The disintegration of Germany after the war is graphically presented, as is its recovery, starting in 1924. But after a brief period of prosperity in what he described as the best equipped genetics laboratory in the world, the rise of the Nazis began. Although he remained at the Kaiser Wilhelm Institute until 1935, he saw what was coming, and began looking for a position abroad. When he was fired, he had already arranged for a lecture tour in the U.S. After some anxious months, he was called to the Berkeley campus of the University of California, which he describes as the "most congenial and charming of all universities on earth." Even here the shadow of Hitler fell, for he was again declared an enemy alien, and was subject to absurd restrictions until he became a U.S. citizen in 1942.

This is an intensely personal and frank narrative. Some readers will object that he sounds vain in some passages, particularly when evaluating his achievements. Those of us who knew and loved this great scholar knew that this is a misapprehension. He had a generous appreciation of the work of others which is not consistent with vanity. He has simply evaluated his contributions to biology honestly, without false modesty, as he would evaluate those of a colleague. The book concludes with a list of his publications. These number 248 in all, including 19 books, 133 papers on various aspects of genetics, 4 in protozoology, 27 in cytology, 8 in embryology, 11 in histology and neurology, 7 on cephalochordates, and many miscellaneous papers — enough material for several good careers! Surely, such a man has a right to a sense of satisfaction as he reviews his professional achievements!—EDWARD O. DODSON, University of Ottawa, Ottawa, Ontario.

QUAILS AND PARTRIDGES OF NORTH AMERICA: A BIBLIOGRAPHY. By Charles G. Crispens, Jr. University of Washington Press, Seattle, Washington. 1960. xii + 125 p. $3.25.

Almost two thousand references from 72 journal sources appear in this non-annotated bibliography of 10 species of quails and partridges. Coverage is extensive enough to span all the way from *The Ibis* to the various state propaganda magazines. Foreign language literature has for the most part not been covered, and no attempt was made to include material from Pittman-Robertson Reports. For the chief species, Bobwhite, California Quail and Gray Partridge, the references are classified as follows: food habits and nutrition, life history, mortality factors, management, and reproduction.

This bibliography will be useful to students. It is not with ungratefulness therefore that the following weaknesses are observed. The basis for inclusion or exclusion of references is neither stated nor apparent; as a result one feels that that compilation has no objectivity. While the compiler noted the impossibility of attaining completeness, it is difficult to reconcile his stated hope that the book "will serve as a foundation to be built upon in subsequent years" with his failure to define what his collection represents and what it does not. Which journals were covered, how completely, between what dates, and for what type of literature? While nobody can blame a compiler for avoiding the difficult task of sifting through Pittman-Robertson Reports (though prepared by trained research biologists) it is incongruous that a compiler could use the time and effort thus saved to list articles from dozens of Outdoors Regionalia (written or rewritten largely by Madison Avenue penmen).

The author would have done well to omit several species altogether for they are covered only tokenworth. In fact a more exhaustive treatment of a single species would have been a far more useful contribution. The failure of a bibliographer to use American Ornithologists' Union Check-list nomenclature is inexcusable (both vernacular and scientific names are incorrect in this bibliography) even though many who write in the wildlife field are unfortunately unaware of this standard of usage. The author's use of "Coturnix Quail" in place of the more desirable "Common Coturnix" is consistent with his mixing *Alectoris* and *Perdix* with odontophorine quail. This reviewer deplores the publishing of a purely mechanical bibliography of this kind when there are perfected bibliographic media extant and when creative contributions to journals must be editorially rejected or emasculated in the name of economics. A bibliography of this kind seems an ill afforded luxury but I am glad to keep it as a luxury.—DAVID KENNETH WETHERBEE, Mass. Coop.

Wildlife Research Unit, U. S. Fish & Wildlife Service, University of Mass., Amherst, Mass.

DRAWINGS OF BRITISH PLANTS. Part XIV. Adoxaceae Caprifoliaceae. Rubiaceae. Valerianaceae Dipsacaceae. By Stella Ross-Craig. G. Bell & Sons, Ltd., London. 1960. 30 Plates. 10/6 ($1.47).

This part presents *Adoxa moschatellina*, 8 species in 5 genera of Caprifoliaceae, 17 species in 4 genera of Rubiaceae, 8 species in 3 genera of Valerianaceae, and 5 species in 4 genera of Dipsacaceae, native to the British Isles. In each of the families of this part, there are species which are native, cultivated, adventive or naturalized in this country. Some of the noteworthy species are: *Sambucus nigra*, the large and showy European Elder; the delightful twin flower, *Linnaea borealis; Asperula odorata*, frequently used in the making of May Wine; the Garden-Heliotrope, *Valeriana officinalis*, and Fuller's Teasel, *Dipsacus fullonum*.

The usual level of high quality in representation of perspective views and magnified sections of all of the significant parts and growth characteristics of the species presented is maintained in this part.—L. G. KAVALJIAN, Sacramento State College, Sacramento.

METHODS OF VEGETATION STUDY. By Edwin Allen Phillips. Henry Holt and Co., New York. xvii + 107 p. 1959.

Methods of Vegetation Study is a field manual, done somewhat in the manner of a laboratory manual, apparently for use both by instructors and students. The plan which governs its content is stated on the first page of the Introduction, as follows: "The taxonomist in studying an area makes a list of species which constitute the *flora*. The ecologist begins with the floristic list and by a series of sample plots of observations ascertains the quantitative or qualitative relationships of the various species of the flora, leading to a concept of the *vegetation*. This book is concerned with various methods of sampling and with the treatment of data thus gathered." And further: "This book is in the field of synecology, or plant sociology." In explanation of the varied nature of the content of his book the author has this to say in the Preface: "At present there is a great diversity of concepts and methods in vegetation study. This diversity is proper and characteristic of a young, vigorous, developing field of science, but it produces confusion, particularly to the beginning student." And: "One approach to the teaching of elementary ecology most generally followed is the concentration upon one system to avoid this confusion. This book takes the other approach, the simplified presentation of several different systems from the European continent, Great Britain, and America."

The book contains 25 chapters divided among seven Parts. Fifty-six field exercises are described in the various chapters, from one to thirteen in each. At the end of the book is a list of the literature cited in the text and lists of selected books and journals that might be used in teaching with the manual. There is an Appendix containing lists of equipment and supplies needed for the exercises, and a general Index to the whole book.

Part One is on "Preliminary Survey" and contains a single chapter, on mapping. It is almost entirely on the use of a Bruton-type compass. With

another half-page the author could have described simple plane tabling (there is room for it on page 5), and the chapter would have been greatly improved. Part Two, also with a single chapter, is on "Physiognomic Systems — The Study of Vegetation on a Nonfloristic Basis." Here are field exercises to illustrate use of the life form system of Raunkiaer, the profile diagrams of the British ecologists, and the more recent systems of designation of form categories developed by Küchler and Dansereau. Part Three, on "Floristic Systems," has five chapters. Three of these, with appropriate exercises, are on the obvious questions of the roles of individual species in the total vegetation: "Frequency," "Abundance and Density," and "Cover and Basal Area." The other two chapters are on methods of sampling: "Transects," and "Plotless Methods." Part Four, on "Succession," contains three chapters: "Succession in Place," "Succession Study by Permanent Plots," and "Succession Studies by Surface Profiles and Transects."

Part Five, entitled "Analytic Qualitative Concepts," is a curious one. It is about two pages long and consists of one chapter called "Sociability, Vitality, Periodicity, and Stratification." Shorn of all its unnecessary verbiage and numbers (the authors of its methodologies appear unable to remain unquantitative), it seems to suggest that it might be worthwhile to walk through the vegetation and just look at it, for whatever might be there to see!

The longest section of the book is Part Six, on "The Synthesis of Data from Different Stands." No doubt it was also the most difficult for the author to write, for he had to thread his way through a maze of controversial issues. The thirteen chapter headings will suggest not only the content but also the difficulties involved: "The American Clementsian System," "A British System of Dominance by Scales of Estimate," "Presence," "The Continuum," "Vegetation Formulas," "The Degree of Maturity of a Plant Community," "Community Coefficients," "The Study of Communities on the Basis of Percentage, Density, Frequency, Basal Area, and Size Classes," "The Study of Forest Associations on the Basis of Percentage Canopy Composition in Long Transects," "The Study of Communities by the Use of Contiguous Quadrats," "Study of Communities by Correlation Coefficients," "Reduction of Sampling Error by Stratification of the Sample," "Synthesis of Data on the Basis of Scatter Diagrams." Part Seven, with a single chapter, is on "Artificial Populations."

The book will be useful for those who need a teaching schedule for elementary instruction in synecology, and for those who need a ready and simplified reference book on the complex of methodologies in use or proposed for the study of "vegetation." It is of handy size, easily carried around in a coat pocket. The illustrations, in the form of tables and text-figures, are adequate.—HUGH M. RAUP, Harvard Forest, Harvard University.

ORCHIDS IN AUSTRALIA. By Fred Moulen. Charles T. Branford Co., Boston, Massachusetts. 148 p. 1958. $15.00.

This remarkable book is a photographic record of the beauty of a hundred orchids. The illustrations, reproduced from 35 mm Kodachromes, have captured the color of these prize-winning flowers. The title does not refer to orchids indigenous to Australia, but rather to those favored by Australian fanciers, such as species, varieties, and hybrids of *Cymbidium, Cattleya, Cypripedium, Vanda, Dendrobium, Miltonia,* and *Odontoglossum* among others. The text is restricted to a very general introduction and to brief legends indicating something of the history and growing conditions of the

flowers depicted. It is a book intended for those who revel in the colors and forms found in such profusion among the orchids.—G. T. A. BENDA, University of Notre Dame.

SOUTHERN FOREST SOILS. Edited by Paul Y. Burns. Louisiana State University Press. Baton Rouge 3, La. March, 1960. ix + 132 p. Illustrated. $4.00.

With the advent of intensive forest management in southeastern United States, interest in forest soil productivity in this region has developed rapidly. As a consequence, the theme of the 8th Annual Forestry Symposium sponsored by the Forestry School at Louisiana State University, held in 1959, was southern forest soils. This book constitutes the proceedings of the 1959 symposium.

Topics considered by the 17 authors include the physiography of the southeastern United States, relationships between soils and tree physiology, various aspects of soil moisture and evapo-transpiration, a lengthy discussion of soil productivity estimates by means of site-index determinations, measures for improving productivity of forest soils including use of fertilizers, irrigation and drainage and a provocative inquiry into the biological potential of the southern forest region.

The papers concerned with these different aspects represent, for the most part, appraisals of the pertinent existing knowledge of soil-forest relationships. Throughout the book, the major emphasis is directed toward the use of this knowledge in obtaining maximum production of cellulose. It is not surprising that some of the measures suggested for achieving the desired goal are identical with those used in highly intensive forms of agriculture and horticulture. This approach constitutes a radical departure from the cut-out and get-out attitude that dominated the thinking of most foresters less than five decades ago. It will be very interesting to watch the future development of this field-crop philosophy in forestry.—G. K. VOIGT, School of Forestry, Yale University, New Haven, Connecticut.

THE BIOLOGIST'S HANDBOOK OF PRONUNCIATIONS. By Edmund C. Jaeger. Charles C. Thomas, Springfield, Illinois. xvi + 317 p. 1960. $6.75.

"Terrific vocabulary but poor plot" could well characterize this listing of over 9,000 commonly used and frequently mispronounced terms in the biological sciences. The preferred pronunciation is given for each term with less frequently used but acceptable alternatives following. Although approximately 10 per cent of the terms listed are defined, it is regrettable that the remainder were not.

Obviously, the inclusion of any term in this listing is dependent upon the appraisal of the author. However, there seems to have been a rather arbitrary method of selection used, so that one searches in vain for such commonly mispronounced terms as gila, hirudin, abducens, luciferase, kyphosis and Acanthocephala. Duodenum is listed, but ileum and jejunum are not. One also finds systole but no diastole; homocercal but no heterocercal; Neognathae but neither Agnatha nor Gnatha; Chordate but no Protozoa; anabolism but no catabolism; carapace but no branchiostegite; amphipod and isopod but no crustacean; and Malphigia but no Cowper's. Hominidae is not listed nor is Onycophora, but per - ip′ - a - tus is.

One misspelling was noted — speleology. The spelling given is not acceptable even as an alternative according to Webster's Unabridged International Dictionary.

For one not possessing an unabridged dictionary, this would serve as a convenient reference volume. It seems better adapted to the needs of botanists than zoologists.—BROTHER G. NICHOLAS, F.S.C., University of Notre Dame.

BEEKEEPING IN THE TROPICS. By Francis G. Smith. Longmans. London, 1960. xvii + 265 p. illustrated. $11.25. (Obtainable from Longmans, Green, and Company, New York.)

There exist a multitude of books and bulletins on practical aspects of bee culture, published in many languages and in many parts of the world, and written with varying degrees of competence. At least to one who is not a beekeeper, most of them seem unnecessary, for they are very repetitious.

This book falls in a class of its own for it is the only book designed to be useful to beekeepers of the tropics. The author's experience is primarily in Africa but presumably most of his suggestions would be valuable in other tropical areas. Tropical Africa is blessed by the presence of one of the most vigorous and productive races of the honeybee, *Apis mellifera adansoni;* it seems likely that its introduction to other areas would prove a boon to tropical apiculture. An unusual feature of the book is the information provided on managing bees in small primitive hives. Concrete information on costs, expected profits, etc. under African conditions is included, together with rather detailed instructions on how best to do most of the things that a beekeeper must do.

The non-beekeeping biologist will find interesting the references to the many behavioral differences between various races of *Apis mellifera.* The book as a whole, however, is designed for practical use and is of little interest to the average biologist. Apiculturalists should, of course, have it on their shelves for reference even if they do not live in the tropics.—CHARLES D. MICHENER, The University of Kansas.

TAXONOMY OF FLOWERING PLANTS. By C. L. Porter. W. H. Freeman and Company, San Francisco and London. 452 p., 660 illustrations. 1959. $6.75.

The author of this volume aimed to present a simplified account of the basic principles of taxonomy that would bridge the gap between texts that are really reference books for advanced students and meatless abbreviated treatments. In general he seems to have accomplished this, albeit in a stilted orthodox fashion. In attempting to find a middle ground between detailed presentation and meatlessness, there is always the possibility that too little information will be worse than none at all. This would appear to be the case in some instances in this book.

Part I, comprising the first 142 pages, deals with "the historical and theoretical aspects and with terminology and morphology." The historical account hits the usual highspots of pre-Linnean and Linnean periods, sketches landmarks of progress in the development of phylogenetic systems, and concludes with a brief and scarcely illuminating section on recent developments.

The chapters on taxonomic literature and nomenclature are separated by one on field and herbarium methods. Inasmuch as the last paragraph in the

literature chapter introduces the subject of the International Code, without indicating there that there is more to follow elsewhere, the nomenclature chapter might logically have followed immediately.

In Chapter 6, "Concepts of Taxa," Professor Porter seems to achieve his middleground in regard to the concepts of genera and higher categories. However, his treatment of the species concept, admittedly a difficult one to handle, would seem to be at once too much or too little. Certainly the beginning student of taxonomy will be ill-equipped after such a brief discussion to cope with the concept of the species based on experiment and presented in tabular form taken from Clausen, Keck, and Hiesey.

There is a short chapter on the construction and use of keys which is a highly desirable feature of a taxonomy text. The value of key construction as a teaching and learning device has been under-emphasized. The comparatively great advantages of an indented key over a bracketed key, except to editors and printers (who do not count), is not sufficiently emphasized. The chapter on keys, whereby necessary morphological terminology is used, would be more effective, if it had followed rather than preceded, the chapter on phytography and terminology.

The latter chapter is, with exception noted below, nicely done, well illustrated, and supplemented at the end of the book by a suitable glossary. It includes an exposition on the construction and use of floral diagrams in which the author has worked out some nice refinements.

An instance of what often proves to be a terminological snarl to students is with us again in this book. In the chapter on terminology we find that "Pistils, collectively called the gynoecium, are the female reproductive parts of the flower and occupy a central position. The gynoecium may consist of a single pistil, as in the Lily, of several or many pistils, as in the Buttercup." And that "The basic unit of construction of a pistil is the carpel. . . ." "A pistil may consist of a single carpel, . . . or of two or more carpels partly or completely joined together, . . ." "One can usually determine the number of carpels in a pistil by sectioning the ovary and counting the number of partitions. . . ." "When a pistil is composed of a single megasporophyll, or *carpel*, it is termed a *simple pistil*. When it is composed of two or more carpels that are more or less united, it is a *compound pistil*." It is interesting to note that the basic unit of structure of the pistil is the carpel and that a pistil may consist of a single carpel. By this token is the unit of structure of a pistil also a pistil?

Appropos of these terms we find the following phrases in the keys and in the descriptions of the orders and families later in the book:

gynoecium usually of 3 carpels, which are distinct; the pistil 1, of 1 or more carpels; the pistil 1, of 1 carpel; carpels 2; carpels 3, united; pistil 1, of 2 united carpels; carpels 1-many, separate or united; pistils simple; pistil 1; carpels free; carpels 1 or more; carpels (pistils) usually numerous; pistil of 2-5 carpels; gynoecium of separate carpels; carpels usually 2; carpels usually few; carpels 2-5, often 3.

The example "carpels usually 2;" comes from the description of an order. Each family in that order has "pistil 1, of 2 united carpels." The example, "carpels usually few," comes from the description of an order. The families within that order have "pistil 1, usually of united carpels," and "pistil 1, of 2-5 united carpels." The instructor, if he is old enough, has become inured to this and takes it in stride. The student, if he is kind, smiles sweetly and with the barest suggestion of a shake of the head seems to say, "I have to pass this course. Who am *I* to question?"

Universally nowadays, morphologists consider the carpel the unit of struc-

ture of the gynoecium. A gynoecium may be comprised of a single carpel, two or more separate carpels, or two or more carpels fused in which case it is said to be syncarpous. Pistil appears to be a term that got there first historically. It also appears to have become superfluous but here tradition gets the upper hand. It is scant comfort to a student, whose mind is not initially saddled with a feeling for the sacredness of tradition, to have to wrestle with terminology which has outlived its usefulness, or which is a cause of befuddlement, simply because it has been with us a long long time.

With regard to the concepts of, "simple pistil," and "compound pistil," one might logically (Heaven forbid), consider a sepal as a simple calyx, a gamopetalous calyx as a compound calyx. Similarly, a petal might be considered a simple corolla, a gamopetalous corolla a compound corolla.

This reviewer was pleased to find Professor Porter was not reluctant to let serve the terms hypogynous, perigynous, and epigynous whose derivations are such that their meanings are easily understood, therefore readily taught. This pleasure was, however, soon mixed with some chagrin, for the author's amplification relative to the use of the terms led to an unnecessarily complex analysis for beginners. If each of the three terms has some reasonable separate identity, I am at a loss to reconcile simplicity with the following "Six Basic Morphological Flower Types": 1) the hypogynous flower; 2) The perigynous flower with free hypogynous hypanthium; 3) The perigynous flower with the floral axis expanded continuously; 4) The perigynous flower with adnate hypogynous hypanthium; 5) The epigynous flower without a hypanthium; and 6) The epigynous flower with an epigynous hypanthium.

My criticism of the categories elaborated above is not meant to be construed as favoring the continued wide use of the old "superior" and "inferior" whose omission from the chapter is praised — *even though regrettably they frequently creep in incognito, as it were, in keys and in diagnoses of orders and families later in the book.* Neither does the author consistently, nor even usually, adopt for his own use in keys and diagnoses the six basic flower types outlined above. A cursory tally was made of this with the following results: hypogynous was used alone sixty times; perigynous was used alone fifteen times; epigynous was used alone twenty-nine times; basic type 2 was used once; basic type 4 twice; basic type 5 twice; basic type 6 thrice; some alternative combination of wording of the basic types eight times.

According to the author's own definitions, either directly stated or by inference, the terms perfect and unisexual refer to *flowers;* the terms monoecious, dioecious, polygamous, polygamo-monoecious and polygamo-dioecious refer to *plants.* This is correct. It appears, however, that wherever the author has occasion to use one of the series of terms referring to *plants,* he uses it as applying to *flowers.* For example we find "flowers monoecious or dioecious," "flowers monoecious, dioecious, or polygamous," "flowers polygamous." This is incorrect usage. Certain other authors (some of widely used books) are guilty of precisely this same incorrect usage. Precedent for inaccuracy by no means justifies its perpetuation.

Chapter 9, entitled, "Angiosperms" is devoted to the classification of the group, the criteria used, and some proposed schemes of classification. The question arises why certain of the features of Chapter 2, "Historical Summary," are presented there and not integrated with Chapter 9, or vice versa. The discussions on classification and classification systems in the two chapters referred to seems to be either too little or too much — too little for clarification to the student of the sense of any putative phylogeny; too much not to make the student confused about it all. If there be any reasonably acceptable phylogenetic scheme which has worth in teaching beginning students, let it be

shorn of the vicissitudes of its historical development as interwoven with the historical development of other such schemes. Present it for whatever value it has in getting beginners to think in these terms. Surely it is not necessary to indicate in so doing that this is the only or the last word. Moreover, if it is worthwhile to pursue and ponder phylogeny at all, then it behooves an author of a textbook to present orders and families in whatever phylogenetic sequence he feels has most merit.

The classification of the monocotyledons adopted by the author in "Part II, Selected Orders and Families of Monocotyledons," includes three subclasses which are briefly explained in the chapter on Angiosperms, namely, Calyciferae, Corolliferae, and Glumiflorae. The Calyciferae and Corolliferae are reputedly distinguished by the biseriate perianth of the former, the sepals and petals unlike in texture and color; the perianth of the latter is uniseriate and often petaloid throughout. The Corolliferae includes the Liliales as its basic order, and amongst others the Amaryllidales, the Iridales, the Arecales, and the Orchidales. The author's floral diagrams for *Lilium*, *Narcissus*, *Iris*, *Synechanthus*, and *Orchis*, representatives of the above orders respectively, all clearly show biseriate perianths!

A feature associated with the presentation of representative orders and families which at first seems to offer help for classwork and obviating, one hopes, the necessity for a separate complimentary set of keys, is a simple key for each principal group, *i.e.*, for the Calyciferae, the Corolliflorae, etc. However, having got through the monocotyledons and past the Floriferae in the dicotyledons, the help is at an abrupt end. There are no keys to the orders and/or families of the large Polypetalae and Sympetalae (although there are some keys within orders of these). A set of separate, supplementary keys is necessary after all.

The utilization of space on the pages upon which appear the precise terminological diagnoses of the orders and families is such as to leave plenty of space for the author to have described with *some* feeling, at least, characteristics of living plants representing these categories. As it is, and as is usually the case, the impoverished delineations scarcely permit the thought that Nature ever breathed any life and glory into her creatures. Botanists are said to have imparted an odor to botany. If it is a continuing process, possibly they might yet gild the lily with some fragrance.

During the last several years much has been said by prominent persons in august society meetings and written by them in profound journals about revitalizing the teaching of biology, especially botany. Much of this has emanated from academic or near-academic maestros or near-professional pontificators. A few good healthy swipes have been taken by interested "outsiders." Even smaller fry and run-of-the-mill practitioners occasionally back off to give a few moments thought to whether or not it has anything to do with them.

Just two years ago at this writing, a panel of distinguished systematic botanists published a "Suggested Outline for Teaching Systematic Botany" wherein attention was called to their instructions, viz., " 'the objective is not to replace one orthodoxy by another but rather to stimulate continuing re-evaluation and experimentation in teaching practice,' " and to " 'throw the subject out the window' and start over." In gathering information on outlines of courses being taught around the country the panel could but consider that they (the courses) had as a common denominator, "pious platitudes."

One may perhaps be forgiven for asking whether this is just read into the record. Revitalized teaching, to be sure, begins in the classroom. But unless teachers abandon the practice of having their students use textbooks, a very necessary part of the revitalization must become part and parcel of textbook

writing. A student, as often as not, will come to his first meeting of class with textbook in hand. Not infrequently he will have had interest (or curiosity) enough to have taken a gander at its contents. If it be a textbook in taxonomy, I fear he will have formed a prejudice such that the teacher will have to give it all he has got to revitalize *the student*, for the text is about as likely to have sent bubbles up the nose as a bottle of champagne opened in the days of Theophrastus — who like as not greeted him on page 1.—ROBERT K. GODFREY, Florida State University, Tallahassee.

BEEKEEPING. By John E. Eckert and Frank R. Shaw. Macmillan Co., New York. 536 p., 150 figs. $12.50.

This textbook of apiculture is a much needed revision of E. F. Phillips' "Beekeeping" (Macmillan, 1915). The original has been the standard text in apicultural courses for many years, and it is good to have it brought up to date. There have been many advances during the past 45 years, not only in the applied field of apiculture, but also in our basic knowledge of honey bee biology and behavior. Eckert and Shaw, apiculturists at the University of California and at the University of Massachusetts, have done a commendable job of integrating much of this new information in their revised edition. It should remain the standard text for years to come. I believe that the next edition, if one is contemplated, should contain a section on human sensitivity to bee venom and the problems of desensitization; medical men are likely to look for some discussion of this problem in a book on the honey bee.—KARL V. KROMBEIN, Entomology Research Division, U. S. Department of Agriculture, Washington, D. C.

BIRD PORTRAITS IN COLOR. Text by Thomas S. Roberts, M.D., Revised by Walter J. Breckenridge, Dwain W. Warner, and Robert W. Dickerman. University of Minnesota Press, Minneapolis. 92 pls. 1960. $5.95.

Illustrations of two hundred and ninety-five species, first produced for "The Birds of Minnesota" are again available with a revised text. The plates are well known for the inclusion of sexual, ontogenetic and seasonal variation in plumage. They represent the work of Walter J. Breckenridge, Allan Brooks, Louis Agassiz Fuertes, Francis Lee Jaques, George Miksch Sutton and Walter Alois Weber.

The text material facing each full page plate begins with a brief characterization of each family. For the various species remarks on the distribution and, especially where pertinent, notes on habitat, food, nesting, song and behavior are included. The chief revision of the text has been in matters of distribution and taxonomy, an updating to conform to the last edition of the A. O. U. Checklist. An index contains both scientific and official vernacular names, as well as certain appropriate local or popular names.

Although originally produced for Minnesota ornithologists, the illustrations include a major representation of the avifauna of the Mississippi Valley; thus the book will be useful to naturalists in eastern North America.—ROBERT E. GORDON, University of Notre Dame, Notre Dame, Indiana.

INSTRUCTIONS FOR AUTHORS

In general the author should follow the recommendations of the *Style Manual for Biological Journals* distributed by AIBS at a nominal cost.

Manuscripts should be typewritten, doubled-spaced with ample margins, on one side of 8½ x 11 inch paper. Tables and figures should be placed at the end of the manuscript. Each sheet should be numbered consecutively. The initial page should contain the title, author's name, full mailing address and an informative abstract, not to exceed three per cent of the length of the manuscript. The abstract is published in lieu of a summary. Acknowledgments should be included in the Introduction. Do not underline any words except scientific and generic names.

References in the text should be cited by author and date, e.g., Smith (1960). In the Reference section, they should be listed alphabetically by authors' names. References to periodical literature should contain title, inclusive page numbers and the name of the journal spelled out. Book citations should include author's name, complete title, edition, name and location of publisher, the total number of pages.

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